



This issue of *Lankesteriana* is dedicated to the memory
of the great Mexican botanist and orchidologist,
MIGUEL ÁNGEL SOTO ARENAS
(1963—2009),
tragically murdered in Mexico
on August 27th, 2009

LANKESTERIANA

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MIGUEL ÁNGEL SOTO ARENAS
(JULY 12, 1963 – AUGUST 27, 2009)¹

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Miguel Ángel Soto was born in the city of Torreón, Coahuila, on July 12, 1963. In that city he studied elementary and secondary school at the Colegio Cervantes (1969-1978) whilst he finished high-school at the Universidad Autónoma del Noreste (1978-1980). Parallel with his first studies, Miguel Ángel became involved in the world of plants. His parents loved plants and he inherited great part of this culture. Living in a semi-arid region allowed him to get to know closely one of his favorite groups of plants, about which he acquired ample knowledge: the cacti and succulents. In spite of living in the desert, Miguel Ángel already knew and cultivated his favorite plants, the orchids. Numerous visitors came to his house, even journalists from the local communication media, to see his orchid house.

Later on, Miguel Ángel moved to Mexico City to follow university studies; he majored in Biology at the Faculty of Sciences /UNAM) from 1982-1987. When he finished the credits, he began to write his undergraduate thesis on the orchids of Bonampak, Chiapas. It is suitable to point out that in those times Bonampak was a very remote place, of difficult access and with great extensions of the poorly known Lacandon Jungle. From there, Miguel Ángel and Jorge Meave had to flee in view of the apocalyptic scenes generated by the eruption of the “El Chichón” (or Chichonal) volcano. Miguel Ángel was a perfectionist and, maybe because of this, he did not finish that thesis, although he did publish an article on that results of that sojourn in the heart of the Lacandon Jungle: Soto Arenas, M.A., (1986), *Orquídeas de Bonampak, Chiapas*. *Orquídea* (Mex.) 10(1): 113-132. Miguel graduated some-time later with a new thesis topic, this

time on the genus *Lepanthes*. He wrote the thesis with Gerardo Salazar, and their work served as the basis for the publication of the book: *The genus Lepanthes Sw. in Mexico*, where they published 32 new species, doubling the number of known species for Mexico.

Between finishing his undergraduate studies and finishing his thesis, Miguel Ángel developed numerous projects and publications on orchids. During this period, Miguel spent his days between the Ecology Laboratory (of the Faculty of Sciences, UNAM) and the AMO Herbarium since its inauguration (at that time it was located in La Herradura, in the outskirts of Mexico City, at Eric Hágsater’s house), and his innumerable field trips. He also traveled to the main herbaria of the United States and Europe, studying all the Mexican material on orchids; these voyages being very fruitful in the search of types of numerous species native to Mexico.

Miguel taught some undergraduate courses of the biology, in the Faculty of Sciences, UNAM. Among them: Bio-geography on 10 times (from 1983-1993), General Ecology twice (1987-1988), Systematics (1999), and Natural Resources (2000-2001). He was also professor of the field biology: “Phytogeography of the Montane Cloud Forest of the Sierra Madre in the South of Guerrero” (1983-1984) and “Sinecological Analysis of the Montane Cloud Forest of the State Park of Omiltemi, Guerrero.” (1984-1985).

He directed or co-directed around ten students both of undergraduate as well as graduate levels. Some of them received recognitions for the quality of their thesis; like Rodolfo Solano Gómez whose thesis “The Genus *Stelis* Sw. (Orchidaceae: Pleurothallidinae) in México” (E.N.E.P. Iztacala, UNAM, written in 1993 in co-direction with E. Hágsater, AMO Herbarium) earned an Honors Mention in the Undergraduate

¹ Translation by Carlos Ossenbach.

Thesis Contest of the Botanical Society of Mexico. Similarly, Mariana Hernández Apolinar received First Place in the Undergraduate Thesis Contest of the Botanical Society of Mexico with the thesis "Population Dynamics of *Laelia speciosa* (HBK) Schltr. (Orchidaceae)" (Faculty of Sciences, UNAM, written in 1992 with the co-direction of Irene Pisanty). In October of 1993 he organized very successfully the 5th Latin American Meeting of Orchidology in Xalapa, Veracruz, with the participation of the best known specialists and scholars of orchids of tropical America. In this event an important international exhibition of orchids was also held and of which he was President of the Organizing Committee (Exporquídea Xalapa '93). Miguel Ángel was Vice-President of the Latin American Orchidology Commission (C.L.O., 1991-1993) and President of the same in 1993.

Miguel Ángel was admitted into the Post-Graduate Program in Ecology of the Ecology Institute in 1994. He approved all the credits and passed the doctoral candidacy examination. However, due to his perfectionism, he postponed sitting for his graduation examination until he had the publications he considered were necessary. The thesis he developed was titled "Evolution in *Vanilla* (Orchidaceae): Phylogeny, biogeography and evolution of characters" and he prepared it under the direction of Dr. Elena Álvarez-Buylla (Laboratory of Molecular Genetics and Evolution, Ecology Institute, UNAM). Miguel Ángel's studies on vanillas were not limited to the aspects mentioned in the title of his thesis, since, for example, he also included the study of diversity, genetic variation and the uses historic of the vanillas. From this work interesting results derived, such as the routes and dates of the human dispersion of the cultivation of *Vanilla planifolia* around the world. Unfortunately he did not see the publication of the formal description of several new species and varieties of this genus, like *Vanilla costarricensis* (ined), *V. cribbiana* (ined), *V. dessleri* (ined), *V. martinezii* (ined), *V. sarapiquíensis* (ined), *V. pompona* subsp. *grandiflora* (Lindl.) Soto Arenas (ined), and *V. espondeae* (ined). which are now published in this issue of Lankesteriana, and the corresponding species are included in his contribution to Flora Mesoamericana, which had already been delivered to the editors at Missouri

Botanical Gardens.

From his studies on vanillas the following were published or were left to be published:

- Soto Arenas, M.A. (2006). La vainilla: Retos y perspectivas de su cultivo. (Vanilla: Challenges and Perspectives of its cultivation). *Biodiversitas* 66: 1-9.
- Soto Arenas, M.A. (in press) A new species of *Vanilla* from South America. *Lankesteriana*.
- Soto Arenas, M.A., & R.L. Dressler. (in press) A revision of the Mexican and Central American species of *Vanilla* Plum. ex Mill: Conspectus of morphological and molecular data. *Lankesteriana*.
- Soto Arenas, M.A., K.M. Cameron & E. R. Álvarez-Buylla. (in preparation) Phylogenetic analysis of *Vanilla* Plum. ex Mill. (Orchidaceae: Vanillinae) from congruent morphological and molecular data.
- Soto Arenas, M.A. & P. Cribb. (in preparation). Annotated checklist, identification guide, and a proposal for a new infrageneric classification of the genus *Vanilla* Plum. ex Miller (Orchidaceae, Vanillinae).
- Soto Arenas, M.A. & E. R. Álvarez-Buylla. (in preparation) Notes on the floral biology of Mexican *Vanilla* (Orchidaceae) and the evolution of pollination systems in the genus.
- Soto Arenas, M.A. & E. R. Álvarez-Buylla. (in preparation) Bio-geographic history of the Pan-tropical genus *Vanilla* and the history on the Gondwanic tropical biota.
- Soto Arenas, M.A., J. Cibrián, A., E. R. Álvarez-Buylla, P. Delgado & D. Piñero. (in preparation) Intraspecific variation of *Vanilla planifolia*: what morphology, isozymes, RAPD's, and nuclear DNA sequences indicate.

Miguel Ángel was one of the most knowledgeable people on the orchid flora of Mexico and, in general, of all of Tropical America. He described, alone or as co-author, many new orchids, among many others are: *Phragmipedium xerophyticum*, *Barkeria fritzhaltbingerii*, *Rossioglossum hagsaterianum*, *Sobralia macdougalii*, *Stanhopea dodsoniana*, *S. whittenii*, *Stelis greenwoodii*, *Elleanthus teotepecensis*, *Encyclia calderoniae*, *E. rzedowskiana* and *Oncidium leleui*. Also, he formalized the intra-specific systematization

of *Laelia anceps*, and reclassified (alone or as co-author) numerous species of different genera, among them *Barkeria*, *Elleanthus*, *Rhynchostele*, *Prosthechea*, *Dichromanthus*, etc. He had ample knowledge on the Pleurothallidiinae (*Stelis*, *Acianthera*, *Pleurothallis*, etc.). According to the Missouri Botanical Garden database (W3TROPICOS), there are more than 160 species and sub-species described by him, including new descriptions and reclassifications of some previously published taxa.

Miguel collected more than 11,000 different samples (collection numbers) of plants in Mexico, Guatemala, Costa Rica, Panama and Brazil, which include almost 150 type collections. The main set of his collections as well as his collecting notebooks and personal notes are deposited in the AMO Herbarium (Chinoín Institute, Mexico City). Miguel was a tireless traveler and few people knew the natural habitats of orchids like he did. This is one of the reasons why he was one of the authors that wrote most in the book “The Orchids of Mexico”, and personally supervised its design and edition; the work describes a journey through the ecosystems of Mexico and its orchids, including cultural and conservation chapters. Together with the digital Catalogue (CD) of The Orchids of Mexico it is the most complete popular work there is about Mexican orchids.

One of his already classic works was the publication: Updated Listing of the Orchids of Mexico [*Orquidea (Mexico City.)* 11: 231-275 (1989)]; this list was the basis of the most recent lists about the orchids of Mexico. Jointly with Federico Halbinger he coauthored the book *Laelias of Mexico*, which is one of the most widely cultivated genera by those fond of orchids. Miguel Ángel was executive editor of the journal *Orquidea (Mexico City.)* from 1985 to date. He was also executive editor of some volumes of the *Icones Orchidacearum (Mexico)*, which is probably the best technical reference of the Mexican orchids. He had two other volumes in preparation. Other issues deal with the genus *Epidendrum* throughout the neotropics.

Also, Miguel Ángel collaborated with several of the great current orchideologists including Robert Dressler, Gerardo Salazar, Eric Hágsater, Germán Carnevali, Mark Chase, Cássio van den Berg, Mark Whitten, Phil Cribb, and Ed Greenwood, among

many others. Miguel’s publications are a mandatory reference for orchid scholars, but are also very useful for bio-geographers and evolutionists of the flora of the Neotropics. Due to his great work as a botanist, several species have been dedicated in his honor like: *Lepanthes sotoi* Archila, *Maxillaria sotoana* Carnevali et Gómez-Juárez, *Mormodes sotoana* Salazar, *Stelis sotoana* R. Solano, and some others that are being published in this issue of Lankesteriana.

Miguel was a conservationist since an early age; for example, he was one of the most participative students in the creation of the Reserve of the Pedregal of San Ángel in Mexico City. More recently, he published one of the most complete works on the current situation of orchid conservation in Mexico and participated in many forums related with the conservation of orchids. He was a prominent member of the “Orchid Specialist Group, Species Survival Commission, IUCN” (1993-1997; 1998-2009) and a member of the “Conservation ex-situ Committee” of the same commission (2000-2003). He also participated as counselor of various government agencies like SARH (Ministry of Agriculture and Water Resources), SEDESOL (Ministry of Social Development), SEMARNAT (Ministry of Natural Resources), CONABIO (National Commission of Biodiversity), establishing the most important criteria for the national orchid conservation strategies of Mexico.

Miguel Ángel was a botanist who loved plants and this was reflected in his very good hand in cultivating various families, among which stand out the Crassulaceae, the Cycadaceae and of course, orchids. He was able to form the most important collection of live plants of Mexican orchid species, much of which is now located in the live collection at AMO Herbarium. From the cultivated plants and the field samples, he helped form a DNA bank for research in molecular biology of almost 500 orchid species, and in addition 500 *Vanilla* samples.

In collaboration with E. Hágsater and Cássio van den Berg, he was preparing a phylogeny of the genus *Epidendrum* based both on molecular data as well as morphological and on the vegetative architecture; for that he had sequenced more than 300 species from throughout the neotropics, mostly collected by Hágsater and cultivated at AMO, always careful to have voucher specimens prepared.

He stood out for his attitude, always cooperating with hobbyists and other biologists, which led him to share his knowledge in his field trips, in numerous sessions of the Mexican Orchid Association, and with farmers, particularly those that cultivate vanilla in the states of Veracruz, Oaxaca and Chiapas. He was a proficient lecturer at conferences and scientific seminars, he delivered more than 150 conferences in universities, in botanical gardens, and in botanical and horticultural associations.

Those of us who had the good fortune of having access to his field notebooks, could observe the encyclopedic knowledge he had about the flora and vegetation of Mexico. His acute vision allowed him to find orchids even when driving the car at high speed or in the darkness of the closed forest canopy. It is suitable to point out that he performed as a human altimeter, since he could calculate very exactly the altitude where we found ourselves by only looking at the vegetation around us.

Nora Esponda, the associate secretary of Instituto Chinoín, worked with Miguel for 25 years and developed a close friendship/professional relationship, and describes him as passionate in his work and everything he did, his conversations, his friendship, he was also fun, and worked late into night, sending mails and instructions in the early morning. She claims he

described himself as “neurotic and ill-tempered”, but she never saw him loose control, his character was strong but affable, very demanding of himself, but also very sensitive.

His sister Miriam describes him as a great Chef, it was Miguel who invited the family over for Christmas or some special occasion. He enjoyed cooking a chicken in “mole”, or a leg of venison with herbs in white wine for his friends. His specialty, vanilla ice-cream, was delicious. He moved back to Torreón a couple of years ago in search of tranquility to continue writing about orchids of Mexico, and spend much more time with his parents and two sisters. He had recently traveled with his sisters on a month-long trip through the Huasteca region of San Luis Potosí, Veracruz and into Chiapas; they were amazed how well he knew the country and the most spectacular landscapes. A couple of weeks before his assassination, he had discovered what appeared to be a new species of Pine-tree, on an excursion with his sister Miriam and other friends.

His tragic death occurred on August 27, at his home in Torreón, Coahuila. Miguel Ángel Soto was a controversial character, but without a doubt, he was an extraordinary human being who leaves behind a great void that will be very difficult to fill. We all miss him.

**IN MEMORIAM: MIGUEL ÁNGEL SOTO ARENAS
(1963-2009)**

ERIC HÁGSATER

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We probably first met at one of the monthly gatherings of the Asociación Mexicana de Orquideología in the early 1980's. He and Gerardo A. Salazar were studying biology at the Faculty of Sciences at the UNAM, the National University in Mexico City. Both made their social service mounting specimens and looking after the live orchid collection at the recently founded Herbario AMO (then a part of the Asociación Mexicana de Orquideología). They both proved to have a deep interest in orchids, and decided to pursue a career in orchid research.

Miguel chose to specialize in ecology and taxonomy, and one of his first projects was the epiphytic flora of the region of the archaeological site of Bonampak, Chiapas, where he became particularly well acquainted with the orchids of this tropical, lowland rain-forest. He later participated in several studies of the mesophilous forests of Omiltemi, Guerrero, another site of high orchid diversity, but this time in the higher mountains of southern Mexico, overlooking the Pacific Ocean.

In 1985, after finishing their formal undergraduate studies, that they both became formally employed as research associates in Mexican orchids by the Instituto Chinoín, A.C., in particular in the AMO Herbarium as a base. The objective was to further the knowledge of Mexican orchids from every viewpoint.

Through the years Miguel was able to travel to the most important herbaria in the Americas and Europe, spending sometimes weeks or months at a time, studying and photographing Mexican orchid material. The information contained in the images was transferred to the electronic database at AMO, now covering some 130 thousand records. Most of the slides have been digitalized for easier access. Miguel thus obtained an encyclopedic knowledge of the Mexican orchids. One of his goals was to finish *Orchids of Mexico*, a treatise covering all

the taxonomic and ecological information of all the known Mexican orchid species. This work was done in collaboration with Hágsater, who focused on the genus *Epidendrum*, Gerardo A. Salazar, on terrestrial orchids, and Rodolfo Solano in relation to the Pleurothallidinae; Rolando Jiménez worked on *Oncidium*. Unfortunately, this work, now covering some 1,900 pages remains unfinished.

From the early beginning he stood out as someone willing to learn from others, doing team work and sharing his information with others. This can be seen through the number and variety of thesis he directed, not only with students in Mexican universities, but also at Oxford, England and Riverside, California, as well as in the many papers he co-authored.

Miguel tackled many groups of mainly epiphytic genera, and had a special interest in the Mexican *Laelia*, where he worked together with Federico Halbinger and produced a magnificent revision of all the species and lower taxa, having personally visited with Federico practically each and every locality, to understand each entity.

During several years he worked with Mariana Hernández in the state of Michoacán studying the population dynamics of *Laelia speciosa*, studying how the local farmers cropped the plants for the flower market in ways that could be sustainable. They also followed seedlings on oak trees for several years, recording how many survived each successive year, and how many years it took adult plants to flower for the first time. At the time there were a number of such studies with terrestrial orchid species in Europe and the United States, but very few with epiphytic species in tropical countries. Mariana's thesis was recognized as the best thesis of the year by the Mexican Botanical Society.

Once, while studying the material of *Phragmipedium exstaminodium* he exclaimed "you collected this specimen the day I was born!" Indeed

that June day in 1963 I was visiting the lakes of Monte Bello, a two day jeep-ride from Comitán, through cattle ranches and virgin forests in the highlands of Chiapas. The clear-water, colored-lakes were surrounded by Pine-Oak forests covered with epiphytes, including many orchids, and the amazing lady-slipper with two-foot long petals in full bloom! Miguel and I were deeply aware of the destruction of many natural habitats, mainly due to their transformation into farm-land. That forest however was mostly destroyed by the fires of the very hot spring of 1998, after a deep-cold winter the previous year had killed many of the epiphytes in the trees. He made several field trips to Chiapas to evaluate the state of conservation of *Phragmipedium exstaminodium* for the IUCN. A couple score mature plants were found, but no young seedlings, there appeared to be no natural reproduction.

Miguel, with his interest in ecology, participated in numerous conservation conferences, was a member of the IUCN Orchid Specialist Group, and collaborated with numerous governmental agencies regarding orchid conservation. He prepared the revision of the list of endangered orchids for the Mexican government, prepared monographs of each species, the illustrations prepared by several other botanists at AMO.

Curiously, we never went into the field together during these 25 years of working together. We often discussed plans for the future and worked on many projects, one of them being a new system of infrageneric classification in *Epidendrum*, combining floral, vegetative and molecular data. He sequenced over 300 species of the genus throughout most of its range, most of the samples from plants which I had collected during field trips to Costa Rica, Panama, Colombia and Ecuador. We came to have a good understanding of the variation. His sudden departure leaves this project in chaos.

One of our dreams, since we began working together, was to eventually publish an illustrated book on the Orchids of Mexico. We agreed that it should not be a catalogue, nor a scientific reference book, but rather a narration of the many diverse habitats where orchids can be found, a walk through these forests and savannas. Through the years we gathered material, and he became intimately acquainted with each and

every habitat. The problem was how to finance the edition. I discussed the issue with several prominent editors without finding any way out. Suddenly, in late 2004, at the pharmaceutical company of which Instituto Chinoin is a part, I found myself discussing how we could commemorate the upcoming 80th anniversary of the introduction of its products to the Mexican market. All things came together; we could publish a book of interest to a cultivated public, which was the result of the accumulated knowledge financed by the Institute. Thus we rushed to put a long cherished dream into action. Miguel was at first in charge of putting everything in writing with the help of Gerardo Salazar. The photographs were to be made mainly by Rolando Jiménez Machorro and Marco López Rosas, the illustrators and photographers at AMO. We contracted one of the top scientific publishers in Mexico for the publishing work and asked them to find a suitable translator. As it was evident that we could not include photographs of all the species known to Mexico, we decided to add a CD with as many as we could get. We asked for and got collaboration from all quarters of the world for suitable slides, three dozen photographers participated. Miguel dropped everything else he was working on, including his doctoral thesis on *Vanilla*. He got involved in everything, including the balance and quality of the color selections, and the lay-out of the entire book. We could not find a suitable translator into English, so he made a first translation which Gerardo Salazar and I then worked on with a final revision by Robert Dressler. The book was printed in Japan and arrived in time for the anniversary of the pharmaceutical company. Miguel had put a full year's work into it, often working until mid-night.

It was an immediate success, within a year the 25,000 copies printed in Spanish were distributed and the edition was sold out; those who received the book did not let go of it. It had, however, a surprising unintended effect; it became the standard show-book for sellers of wild-collected orchid species in the local markets in Mexico City and elsewhere. We were dismayed by this. After years of efforts by Miguel Angel to curb this illegal market which depleted populations of mostly desirable horticultural species, growing and collecting species orchids became popular again, with very few sources of propagated plants.

Probably one of Miguel's most cherished projects was *Vanilla*. Aside from being the subject of his doctoral thesis, for which he sequenced some 500 samples from around the world, he discovered that the plant in commerce for its flavor was basically a single clone probably selected by the Totonaca people of the State of Veracruz. He had special interest in working with local communities in recuperating this valuable crop. He searched for the few individual plants with diverse genetic structures. Working in collaboration with several specialists throughout the world he prepared a proposal for a new generic classification, and described a number of species new to science. Seven papers were prepared for publication, unfortunately only one was sent to the publisher. Others pending details are being finished

by the coauthors, and will hopefully be published sometime soon, some in this issue dedicated to Miguel Ángel.

Miguel was working at his home in Torreón, Coahuila, late at night on August 27th. His sister had been helping him till eight o'clock that evening. Suddenly, an assailant entered his house, and after a fierce battle assassinated him. The reasons are still unknown. His body was discovered the following day. He was 47 years old.

His sisters and parents, the whole orchid community, is shocked, as we have all lost a great friend and collaborator, and one of the greatest contributors to the knowledge of orchids in Mexico, not only their diversity, but their ecology and conservation. May he rest in peace.

MIGUEL ÁNGEL SOTO ARENAS: PUBLICATIONS AND MAIN CONFERENCES, 1983-2009

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A NEW SPECIES OF *VANILLA* FROM SOUTH AMERICA¹

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ABSTRACT. A new species from the basin of the Rio Magdalena in northern Colombia is proposed, *Vanilla espondae*.

KEY WORDS: Orchidaceae, *Vanilla*, *V. espondae*, Rio Magdalena, Colombia

During my work with the phylogeny of *Vanilla* it became evident that some specimens represent undescribed species in the genus. The species here described is among the most showy in the genus, suggesting that additional, undescribed vanillas may be remain to be found*.

The taxon is native to South America, where *Vanilla* reaches its highest diversity, and from where much more material is needed. Its relationships are discussed.

Vanilla espondae Soto Arenas, *sp. nov.*

HOLOTYPE: [N.] **Colombia:** Tributary of R. Magdalena, cult. *F. Pérez-Vera* 563, K-L! (illustration voucher).

A *Vanillae trigonocarpae* Hoehne disco labelli papillis verrucisque ornato recedit.

Hemi-epiphytic *herb.* *Stems* apparently thin, terete, smooth, olive green, *ca.* 6.3 mm thick, the internodes as long as the leaves. *Leaf* shortly petiolate, the petiole *ca.* 8 mm long, blade oblanceolate, abruptly acuminate, the apex incurved, base obtuse, the basal margin revolute, coriaceous-fleshy, green, 14.5 x 3.6 cm. *Inflorescence* axillary, a shortly pedunculate

raceme, the rachis congested, with *ca.* 11 flowers, bracts unknown. *Ovary* sub-trigonous conspicuously white. *Flowers:* buds whitish at base, apex green, with the midrib of petals protruding between the sepals; flowers very showy, large, perhaps 12-15 cm diameter when spread out; tepals ivory white, outer, basal surface of the lip ivory-white, mid lobe and throat ivory-white lined with yellow-ochre, papillae of the midlobe yellow; the segments spreading. *Dorsal sepal* recurved, apparently long oblanceolate, acute, perhaps as long as the lateral ones. *Lateral sepals* directed downwards, somewhat falcate, obliquely oblanceolate, obtuse-subacute, base long attenuate, with a prominent axial vein on the abaxial surface and corresponding to the axial groove on the adaxial surface; very smooth, 74-78 x 20 mm. *Petals* spreading, somewhat arcuate, slightly recurved at the apex, narrowly elliptic-oblanceolate, acute-acuminate, convex, apically conduplicate, broader than the sepals, longitudinally keeled on the outer surface, the keel broad and conspicuous, at least 76 long, more than 16 mm wide (not well preserved). *Lip* very showy, forming a long tube, marginally fused to the column at least 2.7-2.9 cm; when spread out trilobed, the lateral lobes scarcely defined with rounded shoulders, oblong-triangular, tapering at apex, *ca.* 28 x 12 mm; midlobe oblong, rounded, the base somewhat narrowed and forming an isthmus, *ca.* 16 x 15 mm; the disc covered by 7 showy rows of papillae, longer towards the apex, the papillae digitiform, up to 3.5 mm high, continuous with warty veins at the apex of the midlobe. *Column* unknown.

ETYMOLOGY: This species is dedicated to my dear friend Mrs. Nora Esponda, administrative assistant at

¹ *Editor's note:* Miguel Angel Soto Arenas passed away August 27th, 2009. We wish to thank Dr. Phillip Cribb for preparing the *camera lucida* drawing of the lip of the holotype, and Rolando Jiménez Machorro for preparing the attached illustration, prepared from a digital image of the holotype and the rendering of the lip by Dr. Cribb.

* *Editor's note:* Additional new species from Mexico and Central America are being described elsewhere in this issue: see Soto Arenas & Dressler, pp. 285—354.

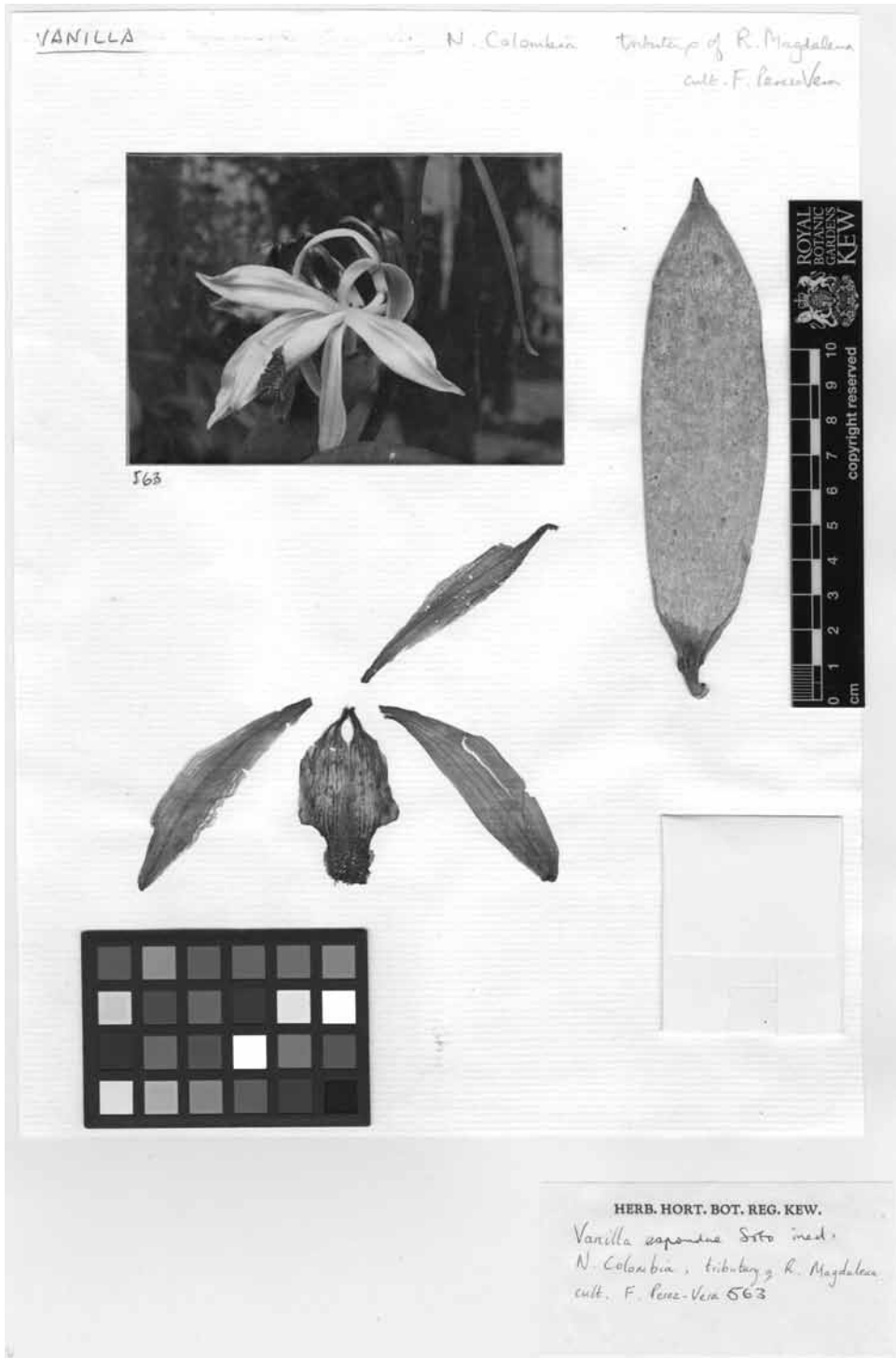


FIGURE 1. Holotype of *Vanilla spondiae* Soto Arenas, by permission of the Keeper, Herbarium, Royal Botanic Gardens, Kew.

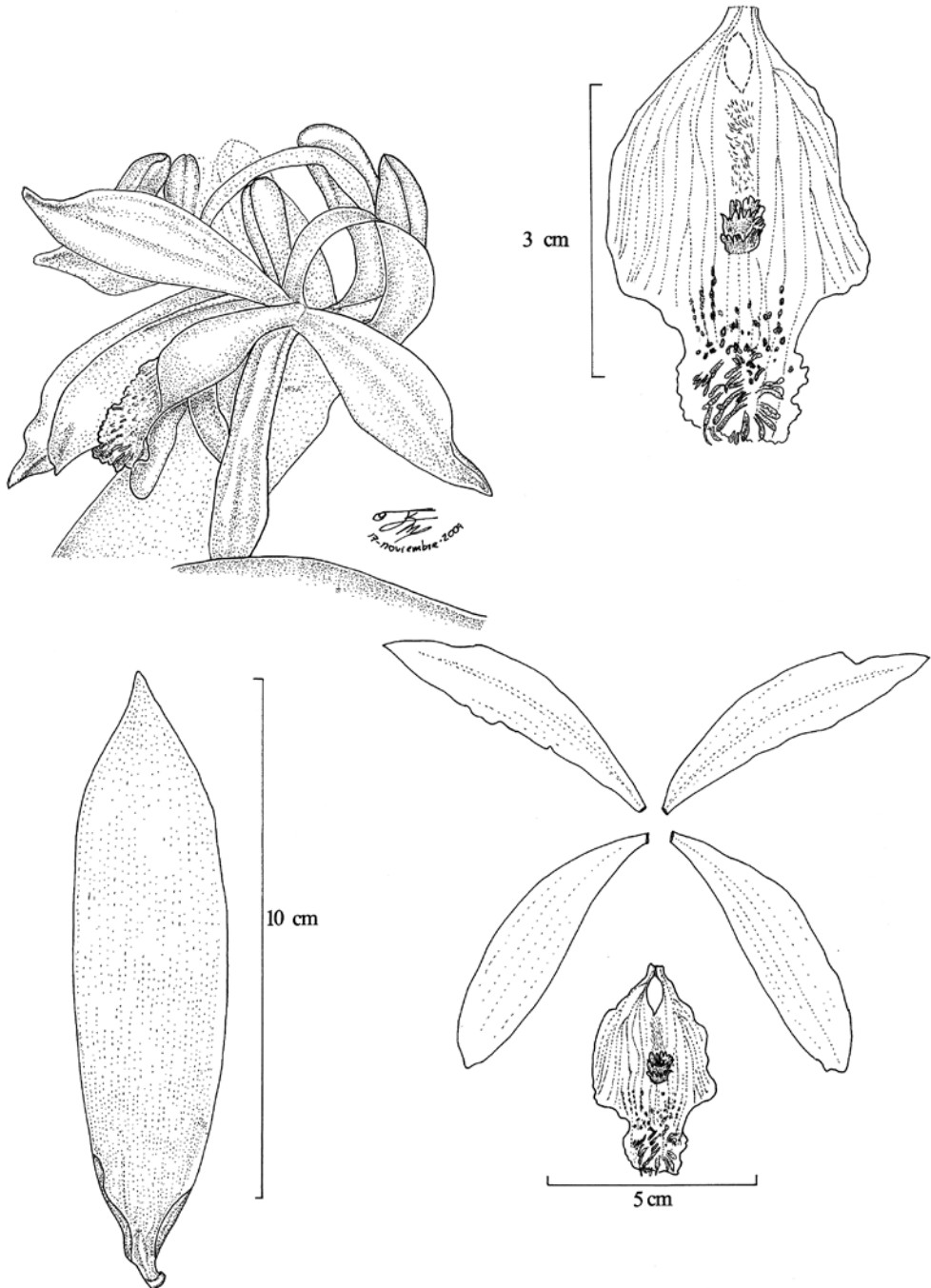


FIGURE 2. *Vanilla espondeae* Soto, prepared from the holotype by Rolando Jiménez M.; the lip based on a *camera lucida* drawing by P. Cribb.

the Herbario AMO. Nora's work is evident in every product of our team and she has been of indispensable assistance during our research work.

DISTRIBUTION: Known only from the type; from the basin of the Río Magdalena in northern Colombia.

This is one of the most beautiful *Vanilla* species. Although it is not closely related to any other *Vanilla*, it could be allied to *V. trigonocarpa*, with which it shares the huge, whitish flowers, and bright yellow disc; *V. trigonocarpa* lacks the papillae and warts on the disc. Other species with similarly adorned lips, like *V. helleri* A.D.Hawkes

or *V. insignis* Ames, have either smaller flowers or green tepals.

The type specimen consists only of a single leaf, a picture of the inflorescence, the 2 lateral sepals, a petal, and the lip, yet the species is so different from any other described species of *Vanilla*, that I have little hesitation in proposing it.

A REVISION OF THE MEXICAN AND CENTRAL AMERICAN SPECIES OF *VANILLA* PLUMIER EX MILLER WITH A CHARACTERIZATION OF THEIR ITS REGION OF THE NUCLEAR RIBOSOMAL DNA ¹

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ABSTRACT. We present a revision of the Mexican and Central American species of *Vanilla*. There are 15 different species in the area; *Vanilla costaricensis*, *V. cribbiana*, *V. dressleri*, *V. martinezii* and *V. sarapiquensis* are here proposed as new taxa, and *V. pompona* subsp. *pittieri* and *V. pompona* subsp. *grandiflora* are recognized at subspecific rank. *Vanilla calyculata*, *V. hartii*, *V. helleri*, *V. inodora*, *V. insignis*, *V. odorata*, *V. phaeantha*, *V. planifolia*, *V. pompona* and *V. trigonocarpa* are also described, illustrated, and their nomenclature, typification, distribution, and other aspects of interest are discussed. Additionally, we include a key to the species. Several Mexican and Central American species of *Vanilla* are closely related to *V. planifolia*, *V. x tahitensis*, and *V. pompona*, the cultivated species of the genus, and these are thus important in plant breeding. We also include a cladistic analysis of nucleotidic sequences of the internal transcribed spacer region of the nuclear ribosomal DNA, showing that this popular molecular marker is of sufficient variation to allow for species discrimination, permitting, with some exceptions that are discussed, the recognition of sterile samples and indicating that it is a good molecular marker to infer the phylogeny of this group. The similarity and relationship between *V. x tahitensis** and *V. odorata* is discussed.

Se presenta una revisión de las especies mexicanas y centroamericanas de *Vanilla*. Existen 15 especies reconocidas en el área. *Vanilla costaricensis*, *V. cribbiana*, *V. dressleri*, *V. martinezii* y *V. sarapiquensis* se proponen aquí como nuevas especies, *V. pompona* subsp. *pittieri* y *V. pompona* subsp. *grandiflora* también se reconocen con status subspecifico. *Vanilla calyculata*, *V. hartii*, *V. helleri*, *V. inodora*, *V. insignis*, *V. odorata*, *V. phaeantha*, *V. planifolia*, *V. pompona* y *V. trigonocarpa* también se describen, ilustran y se discuten aspectos de su nomenclatura, tipificación, distribución, relaciones y otros puntos de interés. Adicionalmente, se incluye una clave de identificación de las especies. Varias especies mexicanas y centroamericanas de *Vanilla* están cercanamente relacionadas a *V. planifolia* y *V. pompona*, las dos especies más frecuentemente cultivadas, y por lo tanto representan un germoplasma importante para este cultivo. Adicionalmente se presenta un análisis

¹ *Editor's note:* Miguel Ángel Soto Arenas passed away August 27th, 2009, before this manuscript was submitted for review. The working manuscript presented here was still unfinished at the moment of his death, and was recovered among Soto Arenas' electronic files. Despite its economic importance, *Vanilla* remains one of the most poorly studied of all large orchid genera, and both the editors and reviewers considered that this publication is an important addition to the orchid and general botanical literature. Ken Cameron, Phillip Cribb, Eric Hágsater, Gerardo Salazar, and Rodolfo Solano did their best to offer corrections and comments to the original draft manuscript. In some instances, however, Soto Arenas quoted preliminary analyses and refers to new taxonomic concepts we were unable to recover. We have not changed the letter of the original manuscript, and such cases are indicated by editor's notes to warn researchers in the future who will find anomalies or have concerns about some of the data.

* *Editor's note:* A paper on *Vanilla tahitiensis* has been published by Lubinsky *et al.*, Neotropical roots of a Polynesian Spice: the hybrid origin of Tahitian vanilla, *Vanilla tahitensis* (Orchidaceae). *Amer. J. Bot.* 95(8): 1040—1047. 2008. In the article, the senior author acknowledges Soto Arenas for suggesting the topic of his PhD thesis.

cladístico de secuencias nucleotídicas de la región de los espaciadores internos transcritos (ITS) de los genes nucleares ribosomales, donde se muestra que las secuencias de este marcador molecular ampliamente utilizado son específicas, lo que permite, salvo algunas excepciones que se discuten, el reconocimiento de muestras estériles y además lo hacen un buen marcador molecular para estudios filogenéticos en este género. Se comenta la similitud y relación entre *V. tahitensis** y *V. odorata*, y el origen híbrido de la primera.

KEY WORDS: Orchidaceae, *Vanilla*, *Vanilla calyculata*, *V. harti*, *V. helleri*, *V. inodora*, *V. insignis*, *V. odorata*, *V. phaeantha*, *V. planifolia*, *V. pompona*, *V. trigonocarpa*, Mexico, central Americas, new species

The Pantropical genus *Vanilla* Plumier ex Miller is a group of orchid vines with about 107 species (Soto Arenas, 2003; Soto Arenas & Cribb, 2010). *Vanilla* is an ancient genus (Chase, 2001; Cameron, 2000, 2003) and the largest in the subfamily Vanilloideae (Soto Arenas, 2003). Some *Vanilla* species are grown as the source of an extract for flavoring and perfumery, especially *Vanilla planifolia* Jacks., with *V. x tahitensis* J.W. Moore and *V. pompona* Schiede being much less cultivated (Correll, 1944; Purseglove, 1975). Vanilla exports generate US \$60-80 million in foreign exchange for producing countries (Smith *et al.*, 1992), perhaps more at present, and it is the most profitable crop of the warm tropics.

The culture of *V. planifolia* and *V. pompona* originated in Mexico, probably in northern Veracruz (Bruman, 1948). Although frequently cited as native of Mexico and elsewhere, there were until recently very few records of *V. planifolia* from wild populations, and its precise original distribution is uncertain (Soto Arenas, 1999). Many *Vanilla* species are similar to *V. planifolia* in floral and vegetative traits, and abundant material in herbaria, both flowering and sterile, is usually misidentified as *V. planifolia*. Even some Mexican plantations planted with wild Oaxacan *Vanilla* vines include a mixture of *V. cribbiana*, *V. insignis*, *V. odorata*, and *V. pompona*, besides the true *V. planifolia*. Similar "mixed" plantations occur in Ecuador (P. Lubinsky, pers. com.) and Guatemala (Beza, pers. com.).

It is well-known that *Vanilla* has peculiarities that make it a taxonomically difficult genus (Wood, 2003), mostly due to the scarcity of flowering material (a result of the gregarious, ephemeral flowering, usually at the top of the forest canopy), the huge vegetative variation and phenotypic plasticity characteristic of

the hemiepiphytic growth habit (e.g. leafy and leafless shoots and differently shaped leaves on the same individual plant as in many hemiepiphytic aroids; Putz & Holbrook, 1986; Ray, 1990), the poor preservation of the membranaceous, strongly three-dimensional flowers make them difficult to study, the notable floral similarities between many species, in part due to the pollination by Euglossine bees (which permits the maintenance of species with little morphological differentiation but with different floral fragrances (in other genera of orchids); Williams, 1982), and the problems derived from the less than perfect quality of type specimens. Additionally, some species are very rare, with sparse populations, and the vines are long-lived perennials that only flower when they have attained considerable size. Small pieces of these plants may be transplanted to greenhouses or gardens, but few of them ever attain the size and strength to flower. There are abundant data that indicate that *V. planifolia* is in danger of extinction in Mexico (Soto Arenas *et al.*, 2004). Scarcity of material can be illustrated by the flowering behaviour of the only Mexican population of *V. harti*, which was found in anthesis only after 7 years of observations. *Vanilla helleri* and *V. martinezii* are each known only from two flowering collections, while *V. costaricensis* and *V. sarapiquensis* are each known from a single pressed specimen. *Vanilla phaeantha* and *V. helleri* are here reported for the first time from Mexico, based on sterile material, whose ITS sequences match with properly identified material of these taxa. Most cultivated specimens of *Vanilla* in botanic gardens and living collections never produce flowers and therefore cannot be identified.

Vanilla plantations face several agricultural problems, the most important being the root rot disease caused by *Fusarium batatis* f. *vanillae* (Childers *et al.*, 1959). It has been suggested that susceptibility to root rot is perhaps due to a narrow

* Véase la *Nota del Editor* en la página anterior.

genetic variation, and that is to be expected in this crop due to its vegetative propagation (Purseglove, 1975; Purseglove *et al.*, 1981; Smith, *et al.*, 1992; Soto Arenas, 1999; Cibrián, 1999). A study of the circumscription of the cultivated species, their distribution, variation, and information on their related taxa, or those with which they may be likely confused is a necessary step toward the establishment of a germplasm bank and a breeding program in this orchid in order to enlarge the genetic foundation of the crop. In the absence of a thorough taxonomic revision, and phylogenetic framework, the breeding programs with *Vanilla* have used very distantly related species that are unlikely to produce fruits with commercially interesting aromatic properties (e.g. with *V. aphylla*, or *V. barbellata*).

The taxonomy of the Central American *Vanilla* species has been previously recognized as confusing (Dressler, 1993), and the available regional treatments are not accurate. Bouriquet (1954) revised the entire genus *Vanilla*, including the Central American species, but his study is out of date and he worked only with herbarium material. In “The Orchidaceae of Mexico”, Williams (1951) listed four species as native of the country, one of them, *V. pfaviana* Rchb.f., is actually a synonym of *V. inodora* Schiede. In recent years, Soto Arenas (1989, 1994) reported additionally *V. mexicana* Miller and *V. odorata*. Later, Castillo and Engleman (1993) have cited significant differences in morphology, phenology, and compatibility behavior in the cultivars of *V. planifolia* (which suggested more than one taxon or a strong genetic structure within the species), and additional species have been recognized in Mexico in recent years (Soto Arenas, 2003; Hågsater *et al.* 2005). On the other hand, *V. insignis* Ames (1934) was described from Honduras, *V. helleri* A.D.Hawkes (Heller & Hawkes, 1966) from Nicaragua, and *V. pauciflora* Dressler (Dressler, 1979) from Panama. *Vanilla hartii* Rolfe was reported from several countries of the area (Correll, 1965), and *V. phaeantha* Lindl. cited from El Salvador (Hamer, 1974). McLeish *et al.* (1995) listed three species from Belize; Hamer (1974) listed two taxa from El Salvador, and four for Nicaragua (Hamer, 1984), while Heller & Hawkes (1966) mentioned five from this same country. Dressler (1993) included three species in his ‘*Field Guide to the Orchids of Costa Rica and Panama*’. Dix

and Dix (2000) reported four species for Guatemala. The brief treatment recently published for Costa Rica (Soto Arenas & Dressler, 2003) lists ten species for this country, three of them unnamed, and it is largely based on the present revision.

Special mention is necessary for the enigmatic *V. x tahitensis* J.W.Moore, described from Tahiti, but apparently introduced to the botanic garden at Papeete from Manila, Philippines in 1848, together with the true *V. planifolia* (Pétard 1986: 123; Hermann *et al.* 1989: 20). *Vanilla tahitensis* is very similar in morphology to some Central American taxa, and very different from the Old World vanillas. No confirmed records of it, either wild or cultivated exist from Central America, or in any other American country, but evidence has been presented of its hybrid origin from *V. planifolia* and *V. odorata*.

A study of the historical records, literature, and field work, both in wild populations and plantations, has proven that some of the reports for Mesoamerica are based on misidentifications, some species must be reduced to the synonymy of previously described taxa, and that some other species of the area remain undescribed.

This revision of the taxonomy of Mexican and Central American vanillas, together with a molecular tool may permit the correct identification of material of this area, even if it is sterile. This is an important issue, in view of the necessity of identifying vegetative material of rare, economically important plants that seldom produce flowers.

For most Central American taxa, sequences of the Internal Transcribed Spacers of the nuclear ribosomal DNA (ITS) were obtained and proved to be species-specific with a high level of confidence, therefore, they represent a tool for the identification of sterile or juvenile living material. The ITS analysis is compared with sequences gathered from two larger, more difficult to sequence chloroplast genes (*rbcl* and *matK*) in order to corroborate its utility.

Material and methods

Herbarium and spirit preserved material was studied in most institutions that house Central American orchids (AMO, AMES, BM, BR, CHAPA, CR, ENCB, F, G, GOEL, HEPF, K, INB, LL, MA,

MEXU, MO, NY, P, RJ, SCZ, SEL, UCR, US, UV, W, WU, and XAL.). Efforts were made to study living material and wild specimens were observed in Mexico, Guatemala, Costa Rica, and Panama. Pollination observations and analysis of fragrances by gas chromatography (conducted by Dr. Neil da Acosta, Bush Boake Allen, London) were an additional element in circumscribing some taxa and are presented in detail elsewhere*.

Due to the phenotypic variation and plasticity seen in the vanillas and mentioned above, the descriptions of vegetative features were prepared only from flowering shoots, often under well-illuminated conditions. Stems and leaves of descending (shaded, ground-oriented shoots) are etiolated, often thinner, or even leafless. On the other hand, *Vanilla* flowers frequently show strong shrinkage in flower dimensions after being pressed; for this reason the measurements of *V. cribbiana*, *V. hartii*, *V. inodora*, *V. insignis*, *V. martinezii*, *V. odorata*, *V. planifolia*, *V. pompona*, and *V. sarapiquensis* were taken from living and/or spirit preserved flowers. For the rest of the species the dimensions were taken from pressed specimens, and those of *V. calyculata* and *V. trigonocarpa* also include measurements of living specimens published elsewhere.

In those species in which more than five different specimens (perhaps not necessarily different clones in the case of *V. planifolia*) were available, either in fresh condition or in spirit, the dimensions of flowering features are also given in mean and standard deviation, in order to determine the possible range of variation more accurately. The flowers of all herbarium material examined were boiled or reconstituted in a solution of ammonium hydroxide.

Internal Transcribed Spacer (ITS) sequences of nuclear ribosomal DNA were collected in order to determine if this widely used molecular marker could be a useful tool to identify material. The sampling (see Table 1) does not include *V. costaricensis* nor *V. sarapiquensis* from which adequate tissue samples were not available. A special effort was made to confirm the specific identity of the specimens, even

of some sterile ones. Due to difficulties in preparing vouchers, some samples remain unvouchered; however, several are housed at AMO or MEXU; pictures of other plants are kept in M. Soto's files (which eventually will be deposited in AMO), but no voucher specimens are known to exist for most plants in living collections (e.g. Royal Botanic Gardens Kew, Nancy Botanic Garden, Jardín Nacional de Cuba, Marie Selby Botanical Gardens, Missouri Botanical Garden, Finca La Gavilana), although they were confidently identified from the living material, and locality data may help to eventually confirm the identity of the populations. Sequences of South American specimens of the *V. pompona* complex were also included. Also a sequence of *V. claviculata*, from Puerto Rico, another of *V. barbellata*, from Florida, and another from *V. mexicana* Miller, species reported for our area from unconfirmed records, were also included. The sequences of *Epistephium parviflorum* and *Lecanorchis multiflora* were defined as outgroups. It is unknown which is the sister genus of *Vanilla*, although morphological data suggest that it is likely *Dictiophyllaria*, a poorly known genus which is known only from the type specimen (Soto Arenas, 2003). *Epistephium*, *Clematepistephium*, *Eriaxis* and *Vanilla* form a polytomy in a cladistic analysis of sequences of the plastid gene *rbcl*. On the other hand, *Lecanorchis* (achlorophyllous, and in which amplification of *rbcl* gene has been unsuccessful) was found to be sister to *Vanilla* from analysis of the nrDNA gene 18S, although a more complete sampling of this region places *Epistephium* sister to *Vanilla* (Soto Arenas, unpublished data)**.

DNA was extracted mostly from fresh leaves using a method based on Murray & Thompson (1980), or from leaves preserved in silica gel (Chase & Hills, 1991). Better quality DNA was obtained using liquid nitrogen and adding 2% of PVP to the extraction buffer. *Vanilla* tissues oxidize badly when they are pressed, especially in the Membranaceous species; all attempts to extract DNA from herbarium specimens failed, although bad quality DNA has

* *Editor's note:* The manuscript "Notes on the floral biology of Mexican *Vanilla* (Orchidaceae) and the evolution of pollination systems in the genus" has been found among Miguel Angel's unpublished manuscripts.

** *Editor's note:* It is unclear to which data the senior author refers here.

TABLE 1. Specimens surveyed for ITS scrutiny.

Taxon	Voucher/ Accession number	Country of origin, province/state, locality
<i>Epistephium parviflorum</i>	K. Cameron 794	Br or TR: without precise locality?
<i>Lecanorchis multiflora</i>	K. Cameron [??]	[??]
<i>Vanilla calyculata</i>	J. Linares 3386 (MEXU)	HD: Morazán, El Zamorano
<i>V. calyculata</i>	J. Linares s.n.	HD: Cultivated in Popenoe's house, El Zamorano
<i>V. calyculata</i>	J. Linares s.n.	HD: Moroceli.
<i>V. calyculata</i>	J. Linares s.n.	HD: bought on streets, El Zamorano.
<i>V. calyculata</i>	J. Linares 8531	HD: Lizapa.
<i>V. calyculata</i>	J. Linares s.n.	HD: Moroceli.
<i>V. barbellata</i>	RBG Kew s.n.	without locality data
<i>V. claviculata</i>	L. Rosigaard s.n.	PR: Maricao
<i>V. eribbiana</i>	M. Soto 7940 (AMO)	MX: Chiapas, Chajul
<i>V. eribbiana</i>	M. Soto 8439	MX: Chiapas, Lacanjá-Chanzayab
<i>V. eribbiana</i>	M. Soto 8370	MX: Chiapas, Chajul
<i>V. dressleri</i>	N. Byrd I-4-6	CR: Punta Arenas, Cañaza, F. Don Andrés
<i>V. dressleri</i>	N. Byrd I-D-3	CR: Punta Arenas, Cañaza, F. Don Andrés
<i>V. dressleri</i>	N. Byrd II-C-2	CR: San José, Río Blanco, Pie de la Tijerilla
<i>V. dressleri</i>	N. Byrd II-C-3	CR: San José, Río Blanco, Pie de la Tijerilla
<i>V. grandiflora</i>	M. Pignal R610	BR: Bahía, Catú
<i>V. grandiflora</i>	J. Batista s.n.	BR: Pará, Xingú
<i>V. grandiflora</i>	Y. Veyret 1	GYF: Sinnamary, St. Elie
<i>V. cf. grandiflora</i>	Boussard, JB Nancy 82.3.246	GD: Guadeloupe, without precise locality
<i>V. grandiflora</i>	Philcox & Thompson 7607	GY: cultivated at Kew, without precise locality
<i>V. cf. grandiflora</i>	J. Bot. Nancy.60.3.414	without locality data
<i>V. hartii</i>	M. Soto 8348	MX: Chiapas, Chajul
<i>V. hartii</i>	E. Salas 1 (INB)	CR: San José, Río Savegre, F. Chaca
<i>V. hartii</i>	N. Byrd II-F-1	CR: Puntarenas, Sándalo, Quebrada Terrones
<i>V. helleri</i>	N. Byrd II-F-4	CR: Punta Arenas, Piró
<i>V. helleri</i>	N. Byrd II-D-5	CR: Punta Arenas, Cañaza-Sándalo
<i>V. cf. helleri</i>	M. Soto 8818	MX: Oaxaca, Sta. Maria Chimalapa
<i>V. inodora</i>	M. Soto 7954a (AMO)	MX: Chiapas, Chajul
<i>V. inodora</i>	M. Soto 8626 (AMO)	MX: Jalisco, El Tuito
<i>V. insignis</i>	M. Soto 7668	MX: Campeche, Calakmul
<i>V. insignis</i>	M. Soto 8611	GT: Izabal, Punta Palma
<i>V. insignis</i>	G. Carnevali s.n.	MX: Quintana Roo, La Pantera
<i>V. insignis</i>	J. Linares s.n.	HD: Río Funes (type locality).
<i>V. martiniezii</i>	M. Soto 8601a (AMO)	GT: Izabal, El Estor
<i>V. martiniezii</i>	M. Soto 8602a (AMO)	GT: Izabal, El Estor
<i>V. mexicana</i>	A. Vale s.n.	CB: cultivated at La Habana, without precise locality

TABLE 1. Specimens surveyed for ITS scrutiny (*continues*).

Taxon	Voucher/ Accession number	Country of origin, province/state, locality
<i>V. odorata</i>	<i>M. Soto</i> 8356	MX: Chiapas, Chajul
<i>V. odorata</i>	<i>M. Soto</i> 8797	MX: Oaxaca, Sta. Ma. Chimalapa
<i>V. odorata</i>	<i>M. Soto</i> 8822	MX: Oaxaca, Valle Nacional
<i>V. odorata</i>	<i>M. Soto</i> 7955	MX: Chiapas, Chajul
<i>V. odorata</i>	<i>M. Soto</i> 8365	MX: Chiapas, Chajul
<i>V. aff. odorata (fimbriata)</i>	SEL 1981-17904	SU: without precise locality
<i>V. phaeantha</i>	<i>G. Carnevali</i> 4825	MX: Yucatán, Sotuta
<i>V. phaeantha</i>	<i>M. Soto</i> 9920	PMA: Veraguas, El Higo
<i>V. phaeantha</i>	<i>J. Bot. Nat.</i> 1197-6a	CB: without precise locality
<i>V. phaeantha</i>	RBG Kew s.n.	UK: cultivated at RBG Kew
<i>V. planifolia</i>	<i>M. Soto</i> 7648	MX: Veracruz, Papanla
<i>V. planifolia</i>	<i>M. Soto</i> 8355	MX: Chiapas, Chajul
<i>V. planifolia</i>	<i>M. Soto</i> 8526	MX: Oaxaca, Usila
<i>V. planifolia</i>	<i>M. Soto</i> 8808	MX: Oaxaca, Sta. María Chimalapa
<i>V. planifolia</i>	<i>J. Linares</i> s.n.	HD: Plant cultivated in El Zamorano.
<i>V. planifolia</i>	<i>F. Pupulin</i> 1966	CR: Heredia, Sarapiquí
<i>V. planifolia</i>	<i>N. Byrd</i> I-4-1	CR: Limón, Guapiles, Los Diamantes
<i>V. planifolia</i>	Dressler s.n.	USA: Florida, cultivated at FLAS, paralogous and orthologous sequences
<i>V. planifolia</i>	RBG Kew cf. 1956-25802	UK: cultivated at Prince of Wales Conservatory, without precise locality
<i>V. pompona</i>	<i>M. Soto</i> 8614 (AMO)	MX: Nayarit, El Cuarenteño-El Cora
<i>V. pompona</i>	<i>M. Soto</i> 7632 (AMO)	MX: Oaxaca, San Gabriel Mixtepec
<i>V. pompona</i>	<i>M. Soto</i> 7747 (AMO)	MX: Veracruz, El Pochote, Zentla
<i>V. pompona</i>	<i>S. Cruz</i> sub <i>M. Soto</i> 8777	MX: Veracruz, Los Tuxtlas, Meyacapan
<i>V. pompona</i>	<i>M. Soto</i> 8119 (AMO)	MX: Oaxaca, Ayoziutepec
<i>V. pompona</i>	<i>J. Linares</i> s.n. (EAP)	HD: Moroceli.
<i>V. pompona</i>	<i>N. Byrd</i> I-4-2	CR: Punta Arenas: Pto. Jiménez, F. La Pajuita
<i>V. pompona</i>	<i>N. Byrd</i> I-4-4	CR: Punta Arenas: F. La Lucrecia
<i>V. pompona</i>	Selby 1985-0211A	PMA: without precise locality
<i>V. pompona</i>	<i>M. Soto</i> 9921	PMA: Panamá, Cerro Azul
<i>V. pompona</i>	<i>J. Bot. Nat.</i> Cuba 86-4746	PMA: without precise locality
<i>V. tahitensis</i>	<i>Colin</i> s.n.	FR: originally from French Polynesia
<i>V. tahitensis</i>	Gen Bank AF 391785	PNG: apparently the type of <i>V. hirsuta</i>
<i>V. trigonocarpa</i>	<i>N. Byrd</i> I-E-1	CR: Puntarenas, Piró
<i>V. trigonocarpa</i>	<i>N. Byrd</i> I-E-5	CR: Puntarenas, Piró
<i>V. trigonocarpa</i>	<i>W. Stern</i> s.n.	PMA: Collected by R.L. Dressler in Panama

Abbreviations: BR = Brazil, CB = Cuba, CR = Costa Rica, FR = France, GD = Guadeloupe; GT = Guatemala, GY: Guyana, GYF: French Guyana HD = Honduras, MX = Mexico, PMA = Panama, PNG = Papua New Guinea, PR = Puerto Rico, SU = Suriname, UK = United Kingdom, USA = United States; F = Finca; J. Bot. = Botanic Garden, RBG Kew = Royal Botanic Gardens, Kew.

been extracted from a couple of South American and Asian herbarium specimens of other species. The ITS region, including the 5.8S gene was then amplified with the primers ITS2, ITS3, ITS4, and ITS5 (White *et al.* 1990; Baldwin, 1992) or 17SE and 26SE of Sun *et al.* (1994). PCR reactions were better when 3% of DMSO was added to the cocktail. PCR products were run in low melting point agarose gel and the band cut to be extracted with QIAGEN Gel Extraction Kit (QIAGEN, Ltd.) or QIAquick silica columns (QIAGEN, Ltd.) adding guanidin chloride (35%) to remove primer dimers. Bi-directional sequencing was performed using cycle-sequencing (ABI Prism dye terminator cycle sequencing ready reaction kit, PE Applied Biosystems, Inc.) with the same primers with which they were amplified using different automated sequencers following manufacturer's protocols. Electropherograms were edited using EditView, and the resulted sequences were initially aligned using Clustal x (Thompson, 1995) and adjusted by eye. Although alignment of *Vanilla* species is easy, the alignment with the outgroups is largely ambiguous and alignment is based mostly on the lengths of the regions. Phylogenetic analysis was performed with PAUP* 4.0 (Swofford, 1998) with the following specifications: *Epistephium parviflorum* and *Lecanorchis multiflora* were defined as the outgroups. An heuristic search with equally weighted parsimony analysis. The analysis consisted of 1,000 replicates with SPR swapping and 20 trees saved per replicate, to save time swapping on islands with large numbers of trees and allowing the detection of multiple islands of equally parsimonious trees (Madison 1991). Then another equally weighted parsimony analysis was performed, swapping to completion of all the trees from the previous analysis. This was followed by a bootstrap analysis, holding 10 trees per replicate for 1000 replicates, using SPR swapping and MULPARS. Bootstrap values were obtained from 100 replicates.

Results

We recognize 15 *Vanilla* species in Mexico and Central America. A key and a taxonomic treatment are presented in the following pages. Five species,

Vanilla costaricensis, *V. cribbiana*, *V. dressleri*, *V. martinezii*, and *V. sarapiquensis* are proposed as new species and three subspecies are recognized within *V. pompona* (the typical subspecies, subspp. *pittieri* and *grandiflora*).

Amplification of PCR products was better with primers 17SE and 26SE of Sun *et al.* (1994) and with them only a single band was obtained. Two bands, one probably from an endophytic fungus were sometimes amplified using primers ITS4 and ITS5.

The analysis of nucleotidic sequences resulted in 669 characters, from which 246 were constant, and 271 sites were parsimony-informative. The heuristic search yield a total of 39,090 most parsimonious trees (tree length = 1070). The strict consensus of this tree is presented in Fig. 1.

This tree is largely congruent with phylogenetic analysis based on morphological and molecular characters, either of plastid (*rbcL* gene, Soto 2003; *matK* gene, Soto & Alvarez-Buylla, unpublished), of nuclear sequences (18S and ITS sequences from species from all the world). In all the analysis two main groups of *Vanilla* are recognized. One of them includes the Membranaceous vanillas (*V. inodora* and *V. martinezii* in the tree; *V. costaricensis* and *V. sarapiquensis*, from which DNA was not available belong to this clade). The other lineage of *Vanilla* includes the leafless plus the leafy, non-membranaceous species.

Two very dissimilar sequences of *V. planifolia* were obtained from two different PCR reactions of the specimen *Dressler s.n.* (cultivated at FLAS). One of these sequences is practically identical to other eight sequences of the same species included in the sample. The anomalous *V. planifolia* sequence goes sister to a *V. mexicana* sequence, forming a clade which occupies a basal position to the rest of *Vanilla*. When *Clematepistephium smilacifolium* and *Eriaxis rigida* are included into the analysis, this clade occupies an intermediate position between *Clematepistephium-Eriaxis-Epistephium* and *Lecanorchis* (data not presented). *Vanilla mexicana* is the type species of the genus, and closely related to, even difficult to separate from, other membranaceous vanillas (e.g. *V. martinezii* and *V. inodora*). These anomalous sequences make both *Vanilla* and the defined outgroup non-monophyletic. The *rbcL* (Soto Arenas,

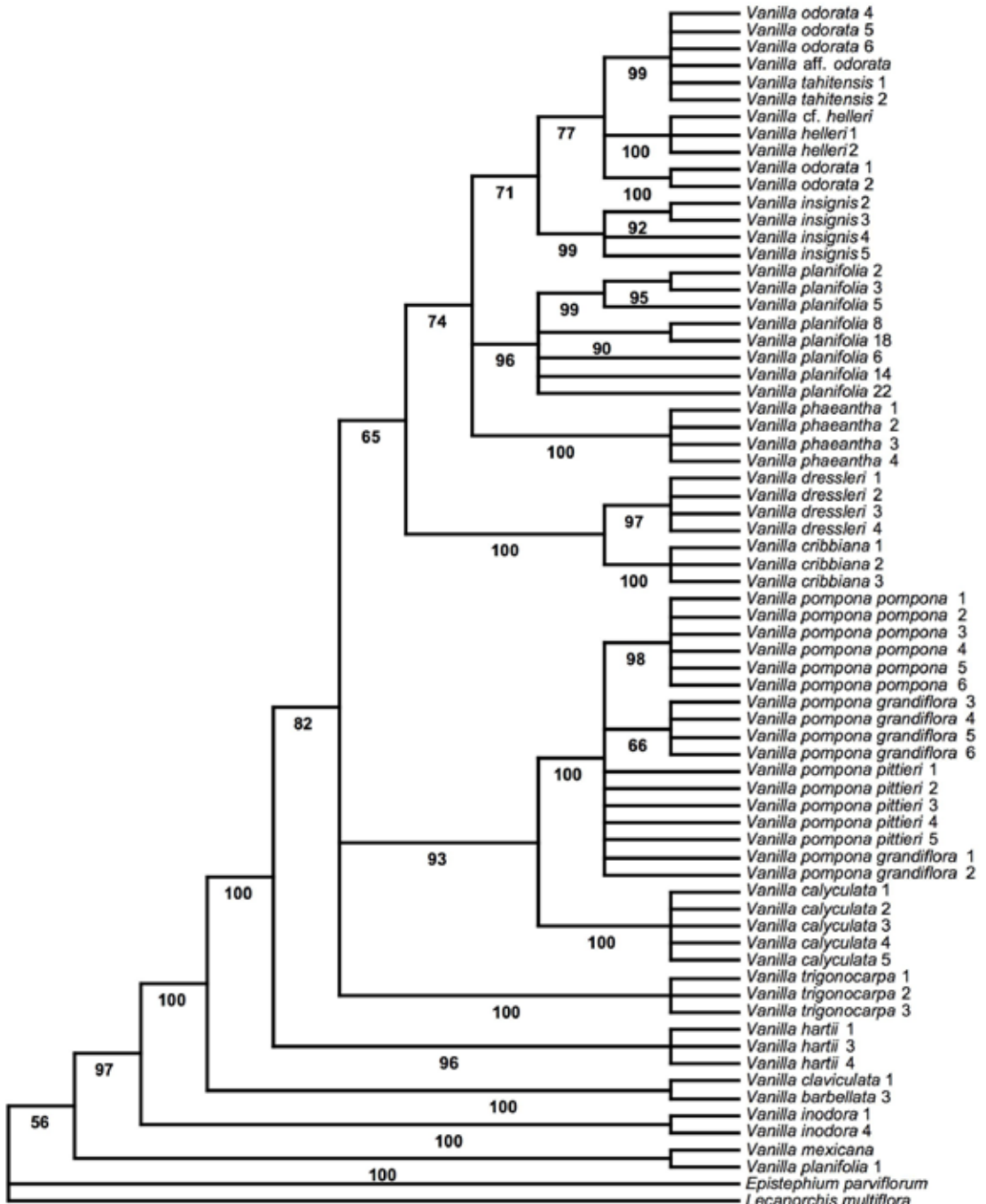


FIGURE 1. Strict consensus from 30,090 minimal trees obtained from ITS sequences of the nuclear ribosomal DNA.

2003), *matK*, and *18S* topologies (Soto Arenas *et al.*, in prep) are incongruent with the position of these two particular sequences of *Vanilla* and we regard them as paralogous ITS copies. Cloning in 10 PGEM a PCR product of *V. cf. kaniensis* Schltr. (a species from New Guinea) yield three different ITS clones which differ only in 1 and 2 DNA bases and are clustered together in the ITS phylogeny, therefore ITS is a very useful identifying tool.

Other paralogous ITS sequences of *Vanilla* (from species of other regions) have occasionally resulted, especially when DNA has been extracted from herbarium specimens or less often from tissues dried in silica gel. No more paralogous copies of American vanillas have been detected, and both included represent the two main lineages in the genus. If they are excluded, both the defined outgroup and *Vanilla* become monophyletic. The paralogous sequences are largely divergent, and therefore easily identified. This is probably because the duplication event that produced them seems to have been previous to the separation of *Vanilla* from their related groups.

The leafless group is not well-documented from Mesoamerica (see discussion in 'Excluded taxa'); a Puerto Rican specimen of *V. calyculata* and another of *V. barbellata* were included. There are no confirmed reports of these species from Mexico or Costa Rica, respectively; in any case, it is rather surprising that leafless taxa are absent in Yucatán, very close, and with similar habitats to places in Cuba where leafless vanillas are present. The rest of the Mesoamerican vanillas belong to the group recognized by Soto (2003) as "American fragrant *Vanilla* spp." Phylogeny of *Vanilla* is discussed in more detail in Soto (2003).

What is important for identification purposes is that ITS sequences are largely species-specific, since the species form monophyletic groups with very high bootstrap support.

The only exceptions are *V. odorata* which proved to be paraphyletic, since *V. helleri* and *V. tahitensis* are nested in it. Two samples from east of the Tehuantepec Isthmus share a different ITS sequence. *Vanilla tahitensis* sequences are not different from most of *V. odorata*, a result which is not incongruent with the hypothesis of a recent hybrid origin of this taxon (between *V. planifolia* and *V. odorata*),

as its morphology suggests. The *Vanilla pompona* complex has a bootstrap value of 99%. All the Mexican samples of *V. pompona* plus two specimens (SEL 1985-0211A and a sequence in the Gen Bank U66819) form a clade with 99% of bootstrap support. Several South American specimens of *V. grandiflora* form a weakly supported (63% bootstrap value) branch, and the rest of the South American specimens of *V. pompona* and the Costa Rican, Honduran, and Panamanian specimens of the *V. pompona* complex form a polytomy at the base. This structure in the *V. pompona* complex is congruent with the distributional disjunctions and suggests that an infraspecific classification of the species is required.

In conclusion, ITS sequences are a very useful tool to separate sympatric, vegetatively indistinguishable vines like *V. planifolia*, *V. helleri*, and *V. cribbiana*, or to identify specimens with juvenile or etiolated vegetative characters. We suspect that one of the reasons for the lack of an important breeding effort in *Vanilla* has been due to the difficulties of identifying material.

The origin of *V. tahitensis* has been much argued. These data indicate clearly that *V. tahitensis* is very closely related to *V. odorata*. *Vanilla tahitensis* is clearly a member of the American fragrant clade of vanilla, characterized by leafy plants and penicillate calluses, and which is absent in the Old World Tropics (as in New Guinea) where the vanillas geographically nearest to Tahiti occur), therefore the hypothesis that it was introduced recently to Tahiti is strongly supported. Since vegetatively it has much broader leaves than *V. odorata*, it is almost certain that it is not conspecific with this species. The flower is larger than in *V. planifolia*, and it is rather intermediate in all traits between *V. planifolia* and *V. odorata*.

These molecular data, and other unpublished data including many more species from other areas, suggest that *V. phaeantha*, *V. insignis*, *V. helleri*, *V. odorata*, and *V. tahitensis* are the closest relatives of the vanilla of the commerce, *V. planifolia*, even much more closely related than *V. pompona* with which it has formed hybrids that are at present cultivated. The close relatives all have fragrant fruits and have different habitat preferences; thus they represent a pool of interesting traits with potential to be incorporated into this crop.

KEY TO THE SPECIES AND SUBSPECIES

1. Leaves thin, membranaceous when dry, sometimes slightly chartaceous, rachis of the inflorescence lax with remote bracts; lip united only basally to the column (< 4 mm), column smooth or basally keeled, but without substigmatic hairs; lip without a penicillate callus formed by a tuft of laciniate scales, instead, the callus may be formed by longitudinal keels, or very fleshy cushions 2
2. Bracts of the inflorescence foliaceous, very large, similar to small leaves 3
 3. Lip distinctly trilobed, midlobe emarginate-bilobed, callus massive, cushion-like *V. inodora*
 3. Lip subentire, truncate at apex, callus made up of 2 prominent axial keels and several warty lateral keels *V. costaricensis*
2. Bracts of the inflorescence scale-like, small (< 1 cm long) 4
 4. Lip ca. 42 mm long, with low callus made up of several axial, longitudinal, warty keels *V. martinezii*
 4. Lip ca. 32 mm long, with a massive callus made up of 2 broad, fleshy, sulcate, apically confluent keels *V. sarapiquensis*
1. Leaves thick, coriaceous to fleshy, chartaceous when dry; rachis of the inflorescence dense with approximate bracts; lip attached to the column up to the stigmatic region, usually > 2.5 cm, column with trichomes on the ventral surface, lip with a penicillate callus formed by a tuft of laciniate, retrorse scales 5
 5. Lip without a clear claw, rather cuneate, strongly trilobed, the midlobe short, transversely oblong and covered by conspicuous, complanate papillae along nerves *V. helleri*
 5. Lip conspicuously long-clawed, claw usually very distinct from the blade, the latter entire to trilobed, the midlobe variously shaped, smooth or variously covered with papillae, trichomes or warts 6
 6. Flowers very large, lip > 10.5 cm long, inflated, margins crenulate-plicate, racemes few-flowered (2-3) *V. trigonocarpa*
 6. Flowers not so large, lip < 9 cm long, inflated or not, margins not crenulate-plicate, entire to denticulate or only plicate; raceme several-flowered, usually with > 6 flowers, often much more 7
 7. Leaves conspicuously shorter than the internodes, lip almost smooth, without conspicuous appendages, except by minute warts at the apical part of the axial veins 8
 8. Leaves acuminate; lip < 41 mm long, subentire *V. hartii*
 8. Leaves obtuse to subacute, sometimes mucronate; lip > 60 mm long, trilobate at apex *V. phaeantha*
 7. Leaves usually as long or longer than the internodes, lip apex covered with papillae, retrorse trichomes or the veins thickened, wavy and complanate-warty 9
 9. Lip fringed or denticulate at margins, with an apical thickening with warts, papillae, or retrorse appendages, flowers mostly whitish-green, weakly scented 10
 10. Stems sulcate, minutely papillose, flowers large, the lip more than 65 mm long, margin long laciniate-fimbriate, midlobe covered by retrorse appendages up to 4 mm high *V. insignis*
 10. Stems non-sulcate, smooth, flowers smaller, the lip less than 65 mm long, margin laciniate, erose or denticulate, midlobe with few (less than 5) retrorse papillae or warty 11
 11. Leaves ensiform, long acuminate; lip margin fimbriate *V. odorata*
 11. Leaves oblong to elliptic, acute or abruptly acuminate; lip margin undulate-denticulate, not fimbriate *V. planifolia*
 9. Lip entire or undulate at margins, without apical thickenings or if present without warts, papillae, or retrorse appendages, flowers mostly cream-yellow, with strong and spicy scent 12
 12. Midlobe of the lip longer than wide, emarginate, flower bell-shaped, with the apex of the tepals reflexed *V. calyculata*
 12. Midlobe of the lip broader than long, truncate to somewhat emarginate, flower trumpet-shaped, the apices of the tepals not reflexed 13

13. Lip rhombic, with thickened, flat veins, leaves cuspidate *V. dressleri*
 13. Lip flabellate, obscurely trilobed, with a longitudinal, cushion-like thickening, leaves obtuse to acuminate 14
 14. Stems 3-5 mm thick, leaves 10-22 x 2.3-7.5 cm; lip apex truncate, entire, ovary and sepals fairly papillose-verrucose *V. cribbiana*
 14. Stems 10-24 mm thick, leaves 22-29 x 8-14 cm; lip margin undulate, ovary and sepals smooth
 *V. pompona*

TAXONOMIC TREATMENT

1. *Vanilla calyculata* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 42-43. 1920.

TYPE: Colombia, Cauca: 1000 m - *M. Madero*, not located; **neotype** (here designated): VALLE: Municipio de Tulúa, Corregimiento Mateguadua, Jardín Botánico, laderas en vía de repoblación natural. Altura 1100 m. Enredadera; sépalos verde claro, pétalos amarillo claro, labelo amarillo intenso, frutos maduros color marrón; muy fragantes. 29 sept. 1984. *W. Devia 815* holo. MO (3245054)!

COMMON NAMES: "Vanilla"

Hemiepiphytic vine, branching, leafy, up to ca. 4 m high. **Stems** flexuose, terete, green, 6-12 mm thick; internodes 7-15.5 cm long. Aerial, free **roots** apparently subterete, pale brownish, up to 8.2 cm long, 2-3 mm thick. **Leaves** sessile to subpetiolate, the petiole up to 7-10 mm long; the blade oblong-lanceolate, rather narrow, the base rounded, the apex acute, coriaceous-fleshy, apparently stiff and xerophytic, the margins slightly revolute, 7.5-21 x 1.7-4 cm. **Inflorescence** a 12-14-flowered raceme, 4.2-6 cm long, rachis terete, green, ca. 4-6 mm thick. **Bracts** widely ovate, obtuse, green, concave, progressively smaller, up to 10 x 6 mm. **Flowers** opening successively, 2-3 open at once, pendant, bell-shaped, very showy, sepals pale green to yellowish green, petals pale yellow, lip deep yellow, ca. 9 cm long; strongly fragrant. **Ovary** terete, smooth, sulcate, the grooves twisted, ca. 4-4.5 mm long, 4 mm thick. **Dorsal sepal** oblanceolate to narrowly elliptic, apex subacute-obtuse, somewhat thickened, subcalyptrate, recurved, base attenuate-subunguiculate, basally canaliculate, convex above, smooth, ca. 12-13-veined, 66-80 x 8-17 mm. **Lateral sepals** oblong to narrowly elliptic, oblique, the lower margin more curved, apex subacute-obtuse, somewhat thickened, subcalyptrate, recurved, basally attenuate-subunguiculate, smooth, ca. 12-13-veined, 67-80

x 12-17 mm. **Petals** obliquely oblanceolate, lower margin more arcuate, apex attenuate, rounded, very attenuate at base, acute, with an axial, flat keel on the abaxial surface, 1 mm wide, ending in a free, conic, blunt, short, 1 mm long process; ca. 11-12-veined, 65-80 x 9-16 mm. **Lip** attached to the column along the margins of the basal half (ca. 41-46 mm), tubular, cymbiform, deeper near the middle; axially grooved on the abaxial surface, the groove well-defined and deep, when spread out 78-90 x 36-45 mm; long unguiculate, the claw apically rugose-papillose on the inner surface, 26 x 3-3.8 mm; the blade trilobed, ca. 36-veined, veins branched, the lateral lobes forming an inflated tube around the column, when flattened widely triangular-semiovalate, margins entire, undulate near the midlobe, ca. 37-39 x 14 mm; midlobe dilated and recurved, approximately transversely oblong, deeply emarginate-bilobed, margins crenulate-undulate, veins conspicuously thickened, 14-16 x 21-26 mm; **penicillate crest** at ca. 41 mm from the base, 4.5 x 3.8 mm, made up by 8-10 flabellate, shortly lacerate-laciniate, retrorse, scales, some of them united to each other along the lateral margins; disc with progressively more thickened veins from the center to the apex of the lip, forming an apical, swollen, low cushion, obclavate in outline, rugose-papillose at the apex, 25-27 x 6 mm, 2-3 mm high; with a group of transversal, yellow-orange hairs at the basal part. **Column** very elongate and slender, subtrigonus-subclavate, slightly sigmoid, 51-55 mm long, ca. 4 mm wide; ventral surface flat and lanuginose at the distal half; apex dilated (6 mm wide) with vertical wings, narrow, triangular-flabellate, undulate, ca. 4 x 1 mm. **Stigma** trilobed, the lobes emergent; rostellum trapezoid-flabellate, 2 x 4.5 mm; lateral lobes transversely oblong-flabellate, 1.2 x 1.8 mm. **Anther** versatile, attached to the wide clinandrium margin by a broad filament, triangular-ovate, truncate-emarginate, 5 x 5 mm. **Fruit** fragrant, 8-15 cm long, apparently thick and trigonous. Fig. 2, 17A.

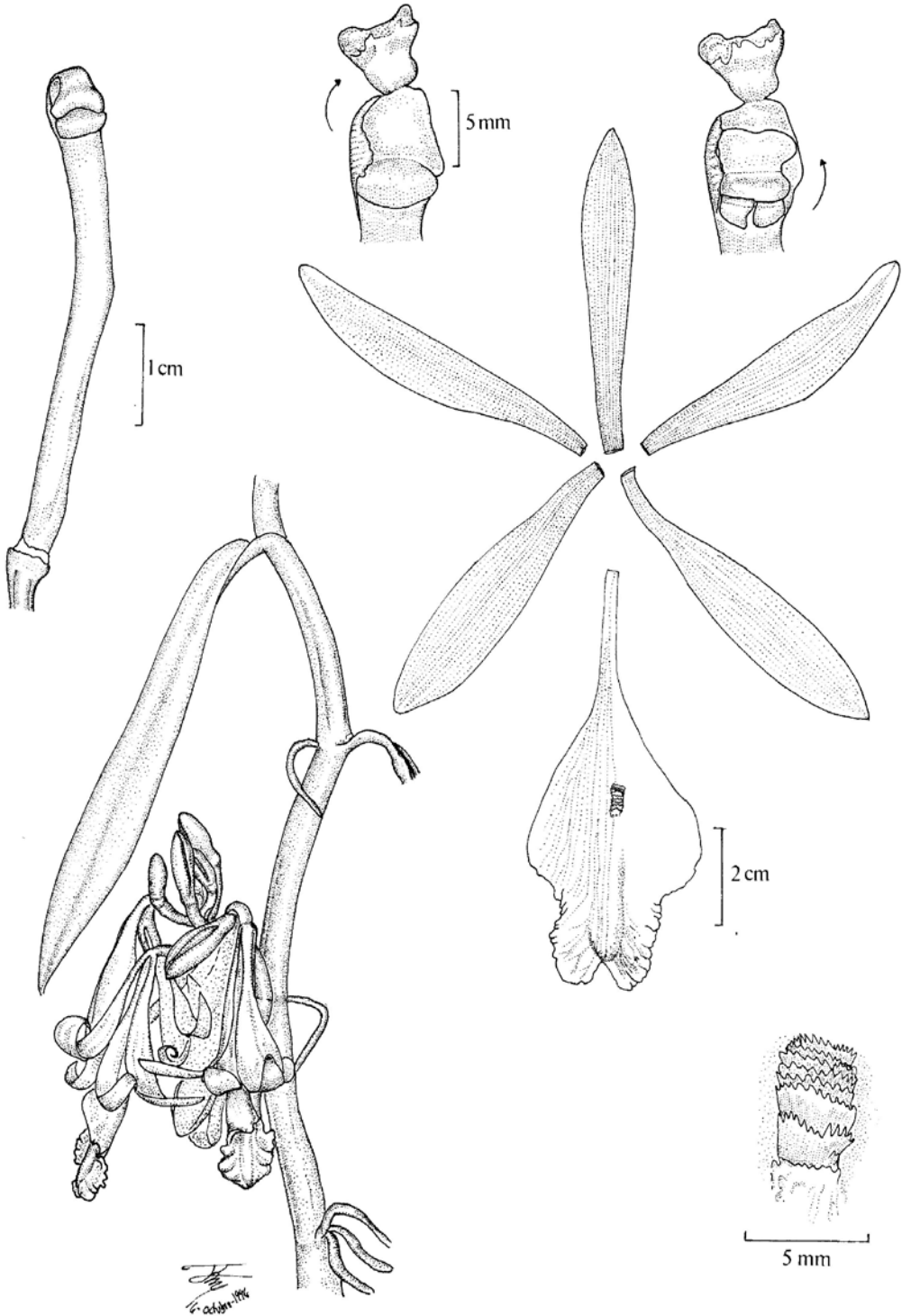


FIGURE 2. *Vanilla calyculata* Schltr. Based on published pictures (Hamer, 1981) and *Devia* 815. Drawing by R. Jiménez.

DISTRIBUTION: Along the Pacific slope of El Salvador, Honduras, Costa Rica, and Colombia; a fruiting specimen from Michoacán, Mexico, may belong here. **ECOLOGY:** Hemiepiphyte at relatively high altitudes (800-1300 m), often in rather dry places. Flowers recorded in April (El Salvador and Honduras) and September-February (Colombia).

The identity of *V. calyculata* has been obscure and no original specimens are known to us. However, Schlechter's description can be applied with confidence to the taxon above described and illustrated in Fig. 1. No other species known from Colombia (*V. colombiana*, *V. dressleri*, *V. espondeae*, *V. hostmanii*, *V. methonica*, *V. odorata*, *V. pompona*, *V. ribeiroi*, and *V. sprucei*) agrees with the description of *V. calyculata*.

The specific epithet makes reference to the calyculus, a minute, cup-like structure sometimes distinguished in some vanillas and more developed in the species of the related genera *Epistephium* and *Lecanorchis*. The calyculus in *V. calyculata* is rather conspicuous when compared with other vanillas, and is more evident in pollinated ovaries that start to swell. Schlechter's description differs from our material of *V. calyculata* in the column described as glabrous instead of pubescent below the stigma (a trait found in all American penicillate Vanillas) and its smaller measurements of the perianth segments. We believe that Schlechter's description could have been based on a bud. However, the calyculus, the sessile, oblong, rather small leaves, the deeply excised midlobe of lip, the pubescent lip claw, the 3-5 thickened midveins on the disc, the unusually high altitude for a *Vanilla* and its strong resemblance with the Brazilian *V. chamissonis* (its sister species, Soto unpublished) suggest that the name *V. calyculata* may be applied to this taxon with confidence.

Vanilla calyculata is distinguished from *V. chamissonis* by its larger, bell-shaped, pendant, yellowish flowers with revolute, flaring tepals, and the longer midlobe of the lip.

Despite its unique characters, specimens of *V. calyculata* have been regarded by Reichenbach and Rolfe (1896; e.g. *Lehmann* 2263) as *V. pompona*. Later it was reported from El Salvador (Hamer, 1974) as *V. phaeantha* Rchb.f. José Linares, from Escuela Agrícola Panamericana has told us that this species is abundant, well-known, and usually confused with *V. pompona* in the dry valleys of central Honduras.

The specimen *O. Pank sub F. Hamer 203* bears peloric flowers where the column has two anthers and two very odd stigmas.

OTHER RECORDS: **EL SALVADOR:** La Palma-Finca El Refugio, río Nanuapa, 1000 m alt., terr. climbing oaks or manzana rosa, collected 3.4.1969. April 11 1969, *O. Pank y F. Hamer 203* AMES(*112862; *113837)! **HONDURAS:** **COMAYAGUA:** Fruit triangular, up to 6 in. long. Climbing in shrubs, thicket along river, plain near Sihuatepeque. 1050 m altitude. 7/23/36, *T.G. Yuncker, R.F. Dawson & H.R. Youse 6045* *AMES(46667)! G! K! *MO(1115382)! NY! **MORAZAN:** flores cremas, bejuco sobre arbustos. Aguas abajo de la Quebrada de Sta. Clara. Alt. 850 m, Abril 28, 1948, *A. Molina 808* *F(1676153)! Bejuco, creciendo sobre rocas y arbustos, flores amarillentas algo fragantes (por la tarde). Quebrada Santa Clara, ca. 2 km al norte del Zamorano, alt. 800 m. Mpio de San Antonio de Oriente. 19 de junio de 1996. *J. L. Linares 3386* MEXU! **EL PARAISO:** Mpio. Morocelí, Quebrada El Cajocote conocida también como El Terrero, 8.7 km al N de Morocelí, por el camino a Mata de Plátano. Veg. riparia, veg. circundante selva baja caducifolia y bosque de pino-encino, 14° 10'10" N, 86°51'06" W, 680 m. Bejuco creciendo sobre Guettarda macrosperma, flores amarillo pálido con el ápice amarillo oro, olor suave y dulce, 29 abril 2004, *J. L. Linares 7313* MEXU! [cf., sterile] "Vainilla", trepadora sobre árboles y matorrales, de Barranco de las Mesas, Alt. 900 m, Agosto 1, 1957, *L.O. Williams & A. Molina 8575* F(1590341)! Open savannah, Las Mesas region near Yuscarán. August, 1960, *H.W. Pfeifer 1454* *US(2563382)! **COLOMBIA:** **TOLIMA:** Fingerdick, bis 5 m lang. Bl. dickfleischig & dunkelgrün. Blt. grünlich meist mit heller Lippe. Früchte bis 8 cm lang. Auf Bäumen in Zavannen -Wäldern bei La Plata. 800-1500 m. 3.12.1882. *F.C. Lehmann 2263* BM! G! *Vanilla*, white and red inside, cultivated *E. Dryander 2379* BM! "Columbien" *Lehmann* W(59043, in part, the flower and probably the right shoot)!

The following sterile specimens may belong here: **MEXICO:** **MICHOACAN:** Hacienda de Coahuayula, Feb. 1901, *G.M. Emrick 16* F(95476)! **COLOMBIA:** [cf., leaves atypically broad] **TOLIMA:** La Plata, 1000-1300, **Lehmann 6278* AMES(14875)!

2. *Vanilla costaricensis* Soto Arenas, *sp. nov.*

TYPE: **COSTA RICA:** ALAJUELA: Llanura de San Carlos. Alt. 200 m., Feb. 20, 1966. Lip white, tepals same green as leaves; vine. Lowland rain forest between Los Chiles and Venecia. *A. Molina R., L.O. Williams, W.C. Burger and B. Wallenta 17565*, holo. CR(062310)! iso. MO(2367689)!

Species *Vanillae oroanae* similis floribus minoribus, labello integro brevior differt.

Hemiepiphytic vine, leafy. **Stems** keeled, 8 mm thick (in dried condition); internodes ca. 12.5 cm long. Aerial, free **roots** dorsiventrally compressed, pale brownish, ca. 2.5 mm wide. **Leaves** petiolate, the petiole canaliculate, ca. 17 mm long, 9 mm wide; blade elliptic, abruptly mucronate, base acute to attenuate, green, membranaceous (in dried condition), 21-22 x 8.7-9.5 cm. **Inflorescence** similar to the vegetative shoots, but smaller, elongate, a 3-4-flowered raceme (probably longer and more floriferous when completely developed), 28-32 cm long, internodes up to 6 cm long; peduncle 15-23 cm, rachis ca. 3 mm thick. **Bracts** foliaceous, subpetiolate, the petiole ca. 3 mm long; blade elliptic, acute-acuminate, base obtuse-rounded, membranaceous, 2.9-7.3 x 1.6-3.4 cm. **Flowers** successive, 2 open at once, with spreading segments, ca. 3.5 cm in diameter; tepals green, lip white. **Ovary** rather sigmoid, 34-40 x 3.5 mm. **Dorsal sepal** strongly twisted and the margins contorted-widely undulate, elliptic, apex acute, rounded, base cuneate, ca. 10 veined, smooth, 41 x 11 mm. **Lateral sepals** narrowly elliptic, acute-subacute, base obtuse, margins undulate, reflexed, smooth, ca. 10 veined, 41 x 10.5 mm. **Petals** narrowly elliptic, apex truncate, notched, base widely cuneate, strongly twisted, widely undulate-contorted, with the lateral margins reflexed, difficult to spread out without distortion, ca. 10 veined, 35.5 x 9 mm. **Lip** attached to the column less than 2 mm, slightly arcuate, almost straight, with the lateral margins erect forming a throat around the column, quadrate-flabellate, entire, apex truncate, obscurely trilobed, the lateral lobes as long as the midlobe, or slightly longer, base rounded-truncate, the apical margin entire to dentate, ca. 26 veined; 24-27 x 20-21 mm; **callus** made up of a pair of flat, broad keels along the axial line, from the base to the beginning of the apical third, then separated in 3 low, erect, congested keels ending at the apex; additional lateral keels with complanate warts adorn the basal half. **Column** relatively short, straight to very slightly arcuate, semiterete, with a dilated apex, 16 mm long; smooth, except by the callus of verrucose keels at base, ca. 5 mm long; vertical wings flabellate, ca. 1.5 x 3 mm. **Stigma** lobed, the midlobe, convex, very prominent, almost perpendicular to the column axis, ca. 2 x 1.5 mm; lateral lobes much smaller, fused in an ovate-

subquadrate, emergent blade, ca. 0.5 mm long. **Anther** galeate, protruding at apex, laterally compressed, 4 mm long, with a long, thick filament 1.2 mm long. Fig. 3.

DISTRIBUTION: Known only from northern Costa Rica. **ECOLOGY:** In lowland rain forest at 200 m altitude; flowering in February.

This species is known only from the type locality and it has been misidentified as *V. mexicana* Miller, a different, closely related species from the West Indies and northeastern South America. *Vanilla mexicana* has a distinctly trilobed lip, with the apex of the lateral lobes slightly above the middle of the lip; in *V. costaricensis* the lip is entire, flabellate, with the apex truncate and just obscurely trilobed, but the lateral lobes of the apex are subequal or slightly longer than the midlobe; additionally, the keels at the apex of the lip in *V. mexicana* are much more conspicuous. *Vanilla costaricensis* has large bracts similar to those of *V. inodora* Schiede, easily distinguished by the cushion-like, axial callus on the lip. Also closely related are *V. guianensis* and *V. martinezii* with much larger flowers, straight sepals, more rugose keels, and shorter inflorescence, with reduced bracts. The species was illustrated by Dr. Rafael Lucas Rodríguez (Rodríguez C. *et al.*, 1986) based on a specimen that has not been located.

The closest relative of *Vanilla costaricensis* is *V. oroana* Dodson of Ecuador. They have similar inflorescences and flower morphology, with the column almost identical. However, *V. oroana* has a longer, relatively narrower, trilobed non-truncate lip, and the surface of the lateral, basal part is minute, but conspicuously more sculptured than in *V. costaricensis*. *Vanilla oroana* flowers are in general much larger.

In the examined material of *V. costaricensis* (and also *V. oroana*) the lateral lobes of the stigma are fused to each other to form an ovate-subquadrate, emergent blade. This is notoriously different from the concave stigma found in other membranaceous (e.g. *V. inodora*). However, observation of this trait is difficult because of the poor preservation of the column, and the large amount of sticky substance in the stigmatic area, visible in fresh material but absent in pressed specimens.

OTHER RECORDS: **COSTA RICA:** ALAJUELA: Llanura de San Carlos. Alt. 200 m., Feb. 20, 1966. Lip white, tepals same green as leaves; vine. Lowland rain forest between Los Chiles and Venecia. A. Molina R., L.O. Williams,

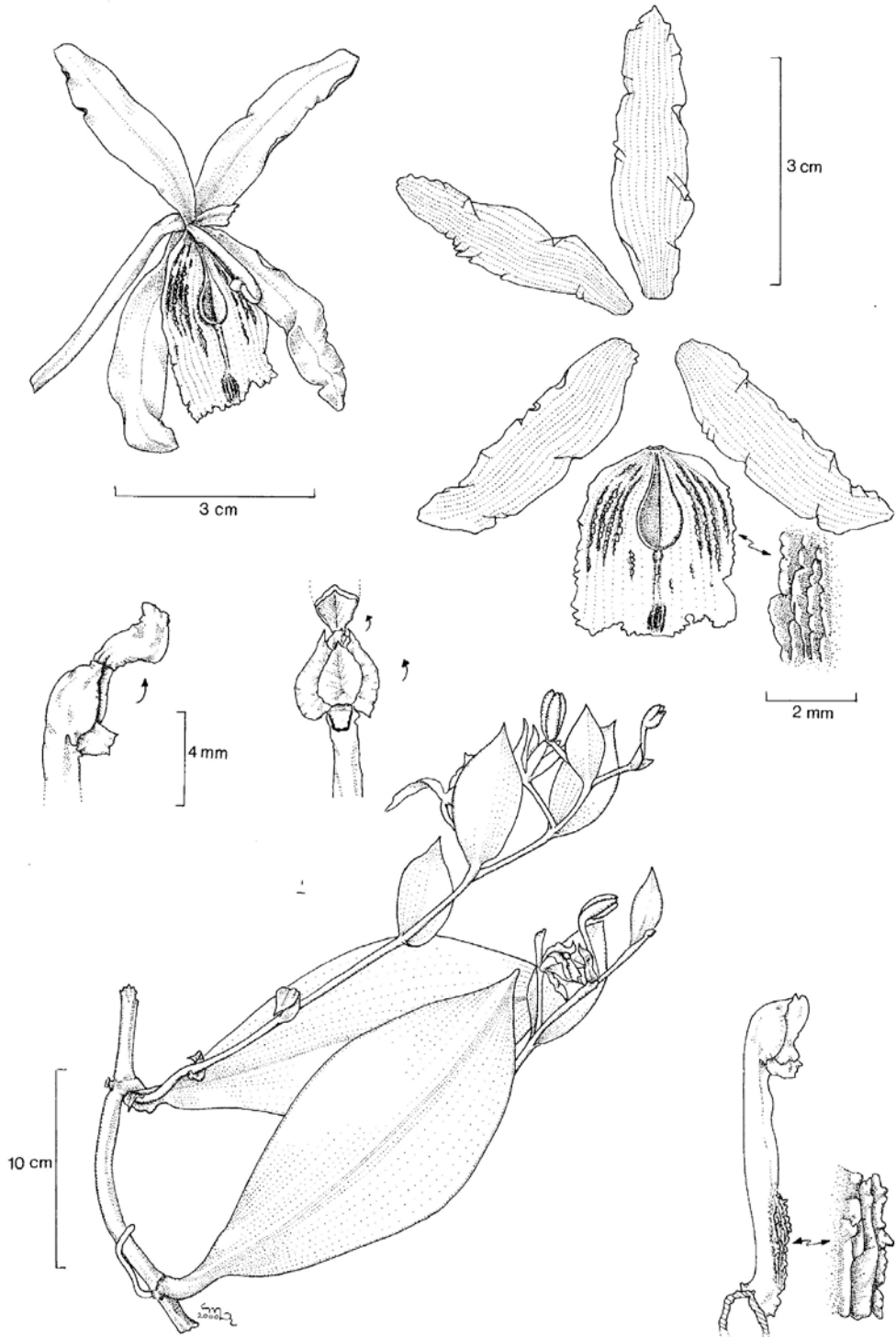


FIGURE 3. *Vanilla costaricensis* Soto Arenas. Based on *A. Molina et al. 17565*, except floral dissection and column based on *A. Molina et al. 17567*. Drawing by M. López.

W.C. Burger and B. Wallenta 17567 *SEL(016793)!
*F(1771938)!

3. *Vanilla cribbiana* Soto Arenas, *sp. nov.*

TYPE: MEXICO: CHIAPAS: Mpio. Ocosingo: Estación de Biología Chajul, en el borde del Río Lacatúm; a 680 m del Puente Hamaca, por la vereda a Arroyo Miranda, ca. 180 m s.n.m., selva alta perennifolia en plano, ca. 8 m de alto, flores con tépalos blanco-cremosos, sépalos verdosos en la superficie externa, labelo atrompetado, amarillo intenso con rayas anaranjadas en las venas, labelo extendido y truncado, sin papilas, no deflexo en el ápice, flores bien abiertas. Fragancia muy intensa y conspicua, a mentol y cítrico. Ovario verde-blanquecino con papilas. 20 junio 1996, *M. Soto 7945 y R. Solano*, holo. *AMO!; iso. K !, AMO (in spirit)!

Vanillae hostmanii primo adpectu similis, sed foliis minoribus, inflorescentiis minoribus paucifloribus, labello obscure 3-lobato, lobo medio distincto, subquadrato, quinque nervis papillosis incrassatis in centro apice ornato versus circa decem nervos in lobos laterales extensos

COMMON NAMES: "Vainilla".

Hemiepiphytic vine, somewhat branching, leafy, up to 12 m high. **Stems** terete, smooth, green, 3-5 mm thick; internodes 3-9 cm long. Aerial, free **roots** pale subterete, brownish, ca. 2 mm thick; attaching, aerial roots conspicuously dorsiventrally compressed, 2-5 mm wide. **Leaves** subpetiolate, petiole 1-1.5 cm long; blade obliquely elliptic to elliptic-oblong, abruptly acuminate-apiculate, stiff, brittle, 10-22 x 2.3-7.5 cm. **Inflorescence** a ca. 10-flowered raceme (rarely up to 30 flowers), 30-37(-110) mm long, rachis 18-22(95) mm long, 4 mm thick. **Bracts** ovate-triangular, obtuse, very concave, progressively smaller towards the apex, up to 8 x 4 mm. **Flowers** successive, 2-3 open at once, with spreading segments, apparently ephemeral, very showy, white-cream tepals, sepals externally cream-greenish, lip deep yellow with orange stripes, ca. 8 cm diameter; fragrance strong, mentholate and citric, similar to that of *V. pompona*. **Ovary** arcuate, dorsiventrally slightly compressed, thickened at the very base, whitish-green, conspicuously papillose,

more densely towards the perianth, sulcate, the grooves twisted, 44-46 mm long, 4-5.5 mm thick. **Dorsal sepal** narrowly elliptic, apex subacute-rounded, subcalyprate, minutely apiculate, base attenuate, flat, apically concave, 9-veined, minutely papillose on the abaxial surface, the papillae in longitudinal rows and forming transverse, undulate rows, very fleshy and stiff; 63-65 x 12.5-13.5 mm. **Lateral sepals** obliquely oblong-elliptic (upper margin curved, lower margin more straight), apex subacute-rounded, subcalyprate, base attenuate, canaliculate basally, slightly convex, apically concave, apex somewhat recurved, margins conspicuously involute, ca. 12-14-veined, minutely papillose in the abaxial surface, the papillae in longitudinal rows and forming transverse, undulate rows, very fleshy and stiff; 60-65 x 12.5-14 mm. **Petals** oblanceolate, very slightly oblique (the lower margin more straight), slightly arcuate, apex obtuse, widely rounded, somewhat thickened at apex, base attenuate, basally canaliculate, slightly concave towards the apex, with an elevated, axial, flat keel on the dorsal surface, ending in a long triangular, flat, free (ca. 2 mm) process; dorsal surface conspicuously canaliculate apically, surface colliculate, the cells in longitudinal rows, 14-veined; with granular, thread-like, somewhat branched inclusions; 64 x 12.5-13.5 mm. **Lip** attached to the column along the margins of the basal half (ca. 28 mm), tubular, trumped-shaped, cymbiform, deepest near the middle; axially grooved on the abaxial surface; when spread out 50-52 x 38 mm; unguiculate, claw with 4 obscure bands of unicellular, minute, elongate, yellow-brownish, trichomes; the blade obscurely flabellate, trilobed, margin conspicuously entire, subtruncate, lip with inclusions similar to those found in the petals; lateral lobes widely and obliquely triangular, overlapping above the column, 33 x 16 mm; midlobe small, subquadrate-ovate, slightly deflexed, smooth, the apex flat, ca. 8.5 x 14 mm; **penicillate callus** made up by ca. 10 congested, retrorse, trapezoidal, laciniated scales, the scales sometimes united to each other along the lateral margins, ca. 5 x 4 mm; the region just after the penicillate callus, smooth, with denser inclusions; with 5 low, rugose, rounded, densely papillose keels confluent in an apical cushion-like thickening, 4-6 secondary, more inconspicuous keels, shorter, not reaching the apex. **Column** elongate, 34 mm long,

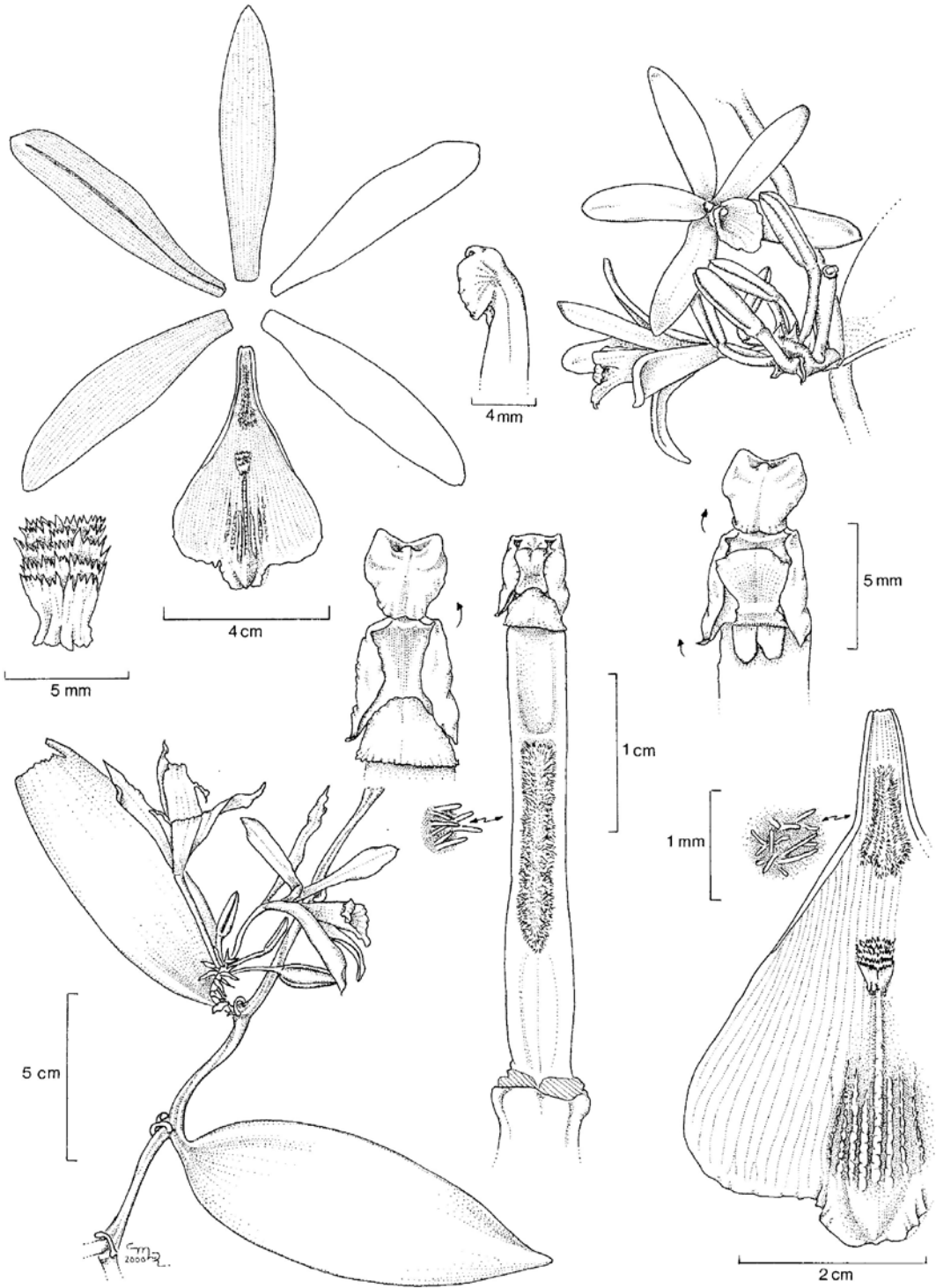


FIGURE 4. *Vanilla cribbiana* Soto Arenas. Based on *M. Soto* 7945. Drawing by M. López.

3 mm wide; ventral surface pubescent-lanuginose at the middle, hairs yellowish; apex dilated, 4 mm wide; vertical wings trapezoidal, the lower margin projected and acute, ca. 2 x 4.3 mm. **Stigma** trilobed, the lobes emergent, with a membranaceous, convex rostellum, 4 mm wide; lateral lobes subquadrate, rounded, ca. 1.2 x 1.2 mm. **Anther** versatile, articulate to the wide, convex, clinandrium, ovoid-subquadrate, 3.5 x 3 mm. **Fruit** short, thick, trigonous in cross section, 10-16 cm long, 1-1.4 cm thick; fragrant when ripe, aroma similar to common vanilla, but weaker. Fig. 4, 16A.

DISTRIBUTION: Known from Mexico (Oaxaca and Chiapas), Guatemala, Belize and Honduras.

ECOLOGY: Hemiepiphyte in rain forest on soils with variable drainage in areas with 2500-4000 mm of rainfall, at 150-350 m altitude. It is the most common *Vanilla* in many areas with tropical rainforest of the Selva Lacandona (Chiapas) and the Petén (Guatemala). It is the only penicillate *Vanilla* in N Central America blooming during the rainy season, in July and August.

Vanilla cribbiana is a member of the *V. hostmanii* group. Like the other members of this complex, it has a slightly trilobed to subentire lip with a disc adorned by some thickened veins. It is different from *V. hostmanii* Lindl. from Amazonia, probably its closest relative, by its smaller leaves, shorter inflorescence with fewer flowers, more defined and subquadrate midlobe of the lip, and only ca. 5 thickened, papillose veins in the center of lip apex, not ca. 10 and spreading to the lateral lobes. From *Vanilla dressleri* Soto Arenas from Costa Rica to Colombia, it is distinguished by its denser raceme, more defined apical lobe of the lip, less conspicuous thickened veins on the disc, papillose-granulose outer surface of the sepals and broader, thicker leaves. *Vanilla ruiziana* Klotzch (synonym *V. weberbaueriana* Kraenzl.) from Peru and Bolivia has a larger, ovate midlobe of the lip which bears 1-3 elevated, axial keels near the apex and the tepals are acute and the sepals neatly calyprate. The flowering period is July-August, at the beginning of the rainy season, and it is also distinct. Vegetatively it is easily confused with *V. planifolia* but the leaves of *V. cribbiana* are usually more elliptic, basally more attenuate, and acuminate at the apex. However, the vegetative differences are difficult to appreciate, and both species are easily confused if flowers are not

available, and especially in sterile shoots grown in shade. Therefore, *Vanilla cribbiana* has been confused with *V. planifolia*, and also with *V. pompona* and even *V. inodora*, in the herbaria and in the plantations.

The fruits of this species are fragrant, and probably of some potential commercial interest, but the vine is not a strong grower, nor does it flower freely, at least in the plantations of northern Oaxaca, where it was introduced when confused with *V. planifolia* (Pérez Mesa, pers. com.). It is pollinated by an unidentified *Eulaema* bee. Beza (com. pers.) reports that the fruits of this species have been cured in Guatemala.

OTHER RECORDS: **MEXICO:** **OAXACA:** cultivated by J. Pérez Mesa at Instituto Tecnológico Agropecuario # 3, San Bartolo Tuxtepec, from plantation in Jaltepec de Condoyoc, near Ma. Lombardo, 24-IV-1997, *J. Pérez sub M. Soto 8504* AMO(in spirit)! **CHIAPAS:** Mpio. Ocosingo, Estación de Biología Chajul, ca. 200 m s.n.m., selva alta perennifolia después de la sabana II, 19 junio 1996, *M Soto 7941 & R.Solano* *AMO(sterile)! Chajul, Camino a Arroyo Miranda. Fruto trígono, ca. 16 cm de largo, 14 mm de grosor, amarillo, rugoso, inflorescencia con ca. 21 flores, 22 junio 1996, *S. Sinaca sub M. Soto 7953A* MEXU! Mpio. Ocosingo, Estación de Biología de Chajul, camino a la Sabana I, selva alta perennifolia en loma, ca. 230 m s.n.m. 13-IV-1997, *M. Soto 8387* *AMO(sterile)! Mpio. Ocosingo, 1.5-2 km al SW de la Colonia Benito Juárez Miramar, sobre la desviación a Tierra y Libertad. Acahual de 18 años derivado de selva alta perennifolia, con *Bursera simaruba*, *Vochysia hondurensis*, 360 m s.n.m., 20°N, 91°12'W, Hierba epífita; fr. inmaduro, 20 agosto 1993, *A. Reyes-García y M. Sousa 2029* MEXU(584270, 584313)! Mpio. Ocosingo, entre Bonampak y el Río Lacanjá, selva alta perennifolia con *Dialium guianense*, *Brosimum* spp., *Ficus glabrata* y *Terminalia amazonia*, 300-350 m s.n.m., abril 2000, *M. Soto 9617, S. Maldonado, P. Schlütter, L. López* AMO(sterile)! [cf., fruit apparently sulcate] a 2 km del Crucero Corozal, camino Palenque-Boca de Lacantúm, Mpio. Ocosingo, 180 m s.n.m., hierba epífita, fruto verde, selva alta subperennifolia, 13 feb 1985, *E. Martínez 10299* MEXU! Mpio de Ocosingo, carretera Palenque-Marquéz de Comillas, Crucero San Javier; selva alta-mediana subperennifolia, inundable, perturbada con *Chrysophylla*, *Vochysia* y muchas epífitas, 16-IV-1997, *M. Soto 8438-8440* AMO(sterile)! **GUATEMALA:** **PETEN:** Fleshy epiphytic vine. Canchacán, in high rain forest of southeastern Petén. July 14 1959. *C.L. Lundell 16457* *LL(x2, buds)! MO(3832548)! "Vianilla", vine, fruits black, fragrant, Dolores, in low forest of pinal about 800 m south of the village on the Machaquila Road, May 18, 1961, *E. Contreras 2333* MEXU(511605)! NY! LL(fruit)! LL(buds)!

“Vainilla” Fleshy vine, fruit green; Dolores, on Río Mopan trail, in high forest, October 17, 1961, *E. Contreras 3063* LL(fruit)! **BELIZE**: STANN CREEK: “vainilla”. Vine; fls., yellow. In high ridge on hill top. Middlesex, 2 July 1939. *P.H. Gentle 2894* *AMES(58082)! K! LL! NY! TOLEDO: Jimmy cut, Alt. 40 m, vive, hanging from tree, no flowering or fruiting, stiff, thick leaves, 1973, *C. Whitefoord 1816* BM! **HONDURAS**: ATLANTIDA: Near Tela. Guaymas. Clambering over tree. March 17, 1923 *O. Ames II 211* AMES(36945, fruit)!

4. *Vanilla dressleri* Soto Arenas, *sp. nov.*

TYPE: **PANAMA**. COLON: End of Pipeline road on Río Agua Salud, 9-10 mi N of Gamboa. Tropical wet forest. Elev. 20-50 m. Vine. Flowers greenish-yellow, lower lip white. Column yellow. Sweet smelling, 15 April 1982, *S. Knapp 4621* & *J. Mallet* (holo. MO 3032052!).

Species *Vanillae hostmanii similis* sed floribus longioribus, labello longiore subintegro anguste obtuso differt.

Hemiepiphytic vine, leafy. **Stems** flexuose, apparently terete, grooved, 3-4 mm thick (in dried specimens); internodes 7.5-11.5 cm long. Aerial, free **roots** terete, 2 mm thick; attaching, aerial roots strongly flattened, up to 4 mm wide. **Leaves** petiolate, the petiole canaliculate, 11-18 mm long, ca. 5 mm wide; the blade oblanceolate, obovate to narrowly elliptic, much larger than the internodes, sometimes slightly oblique, basally rounded to attenuate, apex acuminate-cuspidate, fleshy, chartaceous (in dried specimens), mesophytic, conspicuously pendant in living condition, 10.5-21.5 x 3.0-6.5 cm. **Inflorescence** a 3-10 flowered raceme, rather lax, contiguous bracts distant up to 11 mm; peduncle 15-35 mm long, rachis 15-43 mm long, at least 4 mm thick. **Floral bracts** patent, spreading, concave, widely ovate to elliptic, obtuse, up to 14 x 8 mm. **Flowers** successive, 1 open at a time, big and showy, tepals white to greenish-yellow, lip orange-yellow in the inner surface, fading to white, with brownish veins, column yellow; fragrance clove-like. **Ovary** subterete, straight, thickened towards the apex, bisulcate, the grooves twisted, very inconspicuously and minutely papillose, 42 mm long, 4-5 mm thick; sometimes slightly calyculate. **Dorsal sepal** linear to narrowly elliptic, apex obtuse, rounded, subcalyprate, thickened, with 2-3 warts at the apex of the outer

surface; base narrowed, canaliculate; conspicuously keeled on the outer surface, blade apparently somewhat concave, ca. 13-veined, stiff, fleshy, 72 x 11.5 mm. **Lateral sepals** obliquely linear to narrowly elliptic, apex obtuse, rounded, calyprate, thickened, inconspicuously warty at the apex on the outer surface, base narrowed, concave, blade ca. 11-veined; obscurely keeled on the outer surface, stiff, fleshy, 67 x 12 mm. **Petals** linear to narrowly elliptic, slightly oblique, apex widely rounded, base narrowed, basally concave, with an elevated, axial, flat keel on the outer surface, the keel ending in an acuminate, laterally compressed process, ca. 2 mm long, apex strongly grooved, ca. 10 veined; 68 x 13.5 mm. **Lip** attached to the column along the margins of the basal half (ca. 28 mm), tubular, apparently concave, axially grooved on the abaxial surface; when spread out 65 x 39 mm; unguiculate, the claw canaliculate, lanuginose becoming pubescent towards the blade, 15 mm long, 5 mm wide near the blade; blade subrhombic, margin undulate, pleated, apex obtuse-rounded, very slightly notched, ca. 24-veined; the ca. 11 veins of the apical part thickened and rather warty, with the warts flattened, the central ones rather elevated; the region corresponding to the lateral lobes ca. 36 x 15 mm; the wanting midlobe 10 x 15 mm; **penicillate callus** at 28 mm from the lip base, made up by ca. 12, obtriangular, basally long attenuate, fimbriate scales, 5 x 2.5 mm. **Column** elongate, rather straight, ca. 34 mm long, 3 mm wide; densely pilose on apical 2/3 of the ventral surface, below the stigma; apex dilated, vertical wings oblong, lower apex acute, ca. 1.5 x 3 mm. **Stigma** trilobed, the lobes emergent, rostellum strongly convex, lateral ones apparently very narrow. Fig. 5, 16B.

DISTRIBUTION: Known from Costa Rica, Panama and Colombia.

ECOLOGY: In lowland to submontane (20-1000 m), wet forest. Flowering from March to early June. The species seem to be fairly common, at least in the Río Savagre area of W Costa Rica. The clove-scented flowers suggest a male euglossine bee as pollinator.

ETYMOLOGY: Dedicated to Dr. Robert L. Dressler, authority in orchid evolutionary biology and in orchid floristics of Central America.

This large-flowered species is a member of the *V. hostmanii* group, characterized by its large flowers with

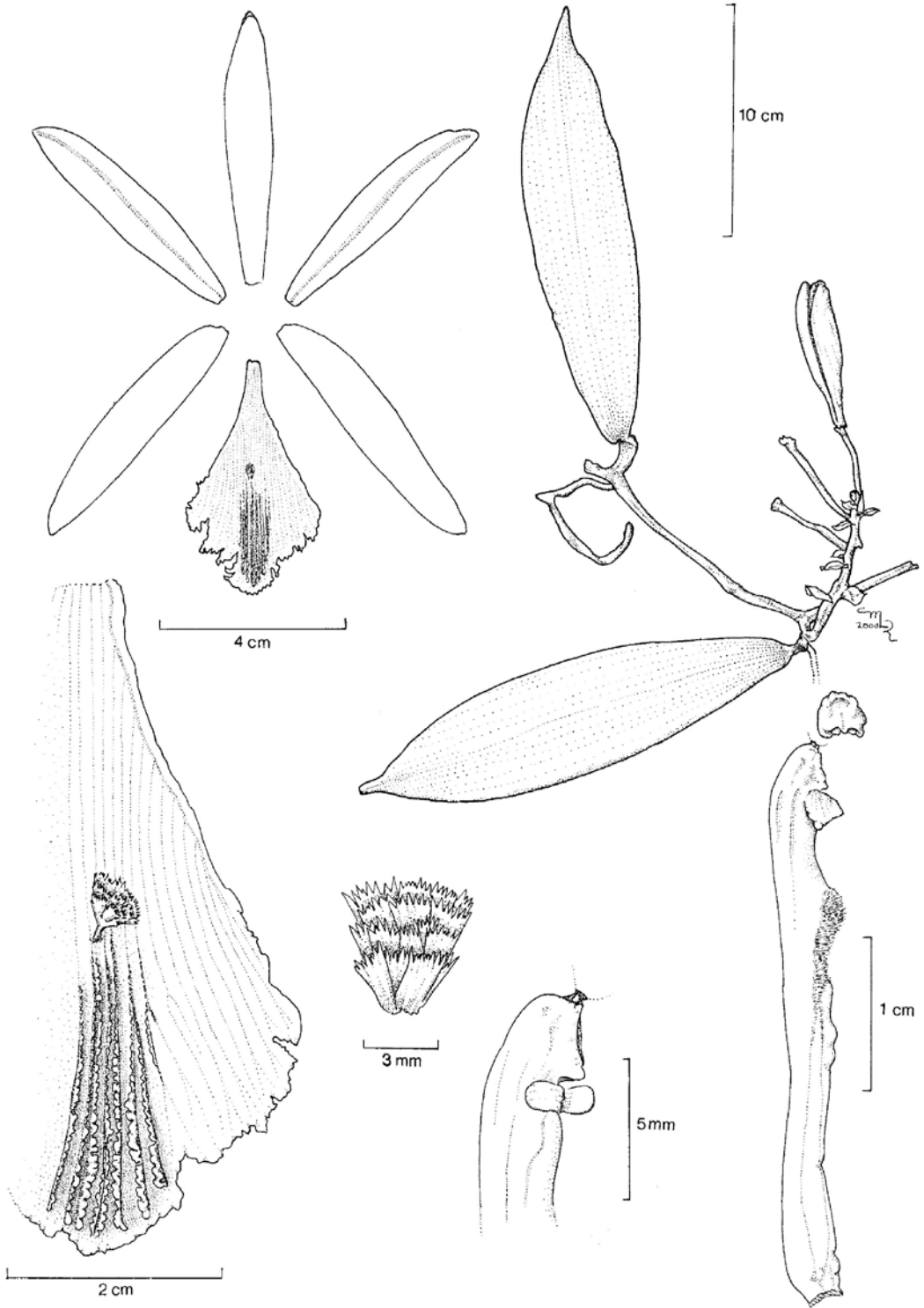


FIGURE 5. *Vanilla dressleri* Soto Arenas. Based on G. McPherson 9196. Drawing by M. López.

scarcely trilobed lips, granulose ovaries and sepals, and the distal veins of the disc thickened. Among the group, it is distinguished by the rather lax inflorescence, with the flowers distant (ca. 1 cm), patent bracts, subtire lip, with the blade subrhombic in outline, and very scarcely papillose sepals; the other members of the group, *V. cribbiana*, *V. hostmanii* and *V. ruiziana* have conspicuously granulose sepals. From *V. cribbiana* it is additionally distinguished by the narrower, thinner leaves which are more long acuminate-cuspidate, more lax inflorescence, less defined apical lobe, veins of the disc more conspicuously thickened, and flowering time mostly in March-May, not in July-August. *Vanilla hostmanii* from Amazonia has very long inflorescences that bear many more flowers (e.g. 40-50) and the leaves are larger, thicker, but not as strongly acuminate-cuspidate. *Vanilla ruiziana*, from Peru and Bolivia has larger, broader, less acuminate-cuspidate, and thicker leaves, but is similar to *V. dressleri* in having rather elevated axial keels of the lip. *Vanilla gardneri* from Brazil has a subacute lip apex and oblong leaves, not cuspidate.

Central American specimens of *V. dressleri* have been previously identified as *V. planifolia* and *V. insignis*, distantly related species, easily separated by the distinctly trilobed lips with well developed retrorse warts.

OTHER RECORDS: **PANAMA:** Flowers yellow green; lip yellow with green patch at apex. Collector, N.H. Williams, Rio Iguanita, fl in cult, 14 April 1978, SEL 56-76-11 [accession num.], *A. Pridgeon s.n. SEL(019244; the leaves; flowers may belong to *V. phaeantha*)! **COLON:** Santa Rita Ridge, southeast of Colón, c. 9°20'N, 79°45'W. Along ridge road, 10-12 miles from Transisthmian Highway, c. 550 m. Vine; perianth white, the lip orange-yellow within basally; flower clove-scented. 21 May 1986. *G. McPherson 9196*, holo. MO(3432756)! **COCLE:** Huge plant purchased in the El Valle market. Flowers pale yellow-green. 6 March 1976. *R.L. Dressler, C. Luer, J. Luer & P. Taylor 768* *SEL(009187)! **COSTA RICA:** **ALAJUELA:** Reserva Biológica Monteverde, Río Peñas Blancas, 10°19'N, 84°43'W, 900 m. Epífita. Flores blancas con amarillo. 7 June 1988. *W. Haber 8471 & E. Cruz* CR INB! MO(3714711)! Reserva Monteverde, Río Peñas Blancas, 10°20'N 84°43'W, 820 m. Bejuco. Flores blancas. 10 June 1987. *W. Haber 7423 & E. Cruz* INB! Upala, San José, Villa Nueva, 11 km al noreste de San José. 10°59'N, 85°07'W, 40 m. Terrestre, trepadora, escandente. Flores en botón verde amarillento. 18 April 1988, **G. Herrera 1840* CR MO(3864177)! **CARTAGO:** 12 km S of Turrialba by air, 4

km SE of Pejibaye along Río Gato. Disturbed primary forest along river. Vine. 700 m alt. 9°48'N, 83°42'W. Vine. 16-17 April 1983, **R. Liesner 14435* MO(3102177)! **SAN JOSE:** Sepals and petals greenish yellow. Lip cream-colored with greenish-brown raised lines. Callus in middle of lip raised and with rows of attached hairs or brushes. Vine. Parque Nacional Braulio Carrillo; Carrillo station, 300-600 m, 31 May-5 June 1980, **C. Todzia 1291* LL! **HEREDIA:** Sep & pet interiorly creamy, faintly greenish, lip embraces column loosely, interior of lip and base yellow, apical 3rd fading to white, leaves succulent, stems single, not branched. Sarapiquí: (April) The lip has been apressed ..., do not reveal the actual appearance of the flowers at complete anthesis, and they have no perceptible odour at 10:30 a.m. Flowers in axillary, stubby branches of from 5 to 8 flowers. Leaves drooping apparently from a rather slender stem, April 1959, **C.H. Lankester 1746* SEL (011365)!. **LIMON:** Reserva Biológica Hitoy Cerere, Valle de la Estrella. Bosque primario, bosque secundario. 700 m Epífita, flores amarillas con blanco, 4 December 1990, *G. Carballo 325* INB! **PUNTARENAS:** Cantón de Golfito. P.N. Corcovado. Valle de Coto Colorado. Estación Esquinas: Sección Esquinas. 08°46'00''N 83°15'00''W, 100 m. Bejuco, frutos verdes. 17 July 1993, *M. Segura 121, F. Quesada & R. Aguilar* INB! **COLOMBIA:** **VALLE:** Río Calima (región del Chocó); La Trojita, 5-50 m alt., Bejuco trepador; flores amarillo blanquecinas, 19 febr.-10 mar. 1944, **J. Cuatrecasas 16550* AMES(71363)! Cordillera Occidental; vertiente occidental: Hoya del río Anchicayá, lado derecho, bajando a La planta, bosques, 200-350 m alt.. Bejuco herbáceo, crasiúsculo; tépalos ocráceo blanquecinos; labelo amarillo claro. 27 sept. 1943, **J. Cuatrecasas 15220* AMES(71364,71365)! **CHOCO:** Parque Nacional de Utría: Colecciones realizadas en la serranía ubicada al este de la ensenada de Utría, en un recorrido oeste-este, entrando por la casa de la Señora Ana Elida (Mesica) siguiendo la trocha que conduce al acueducto cruzando por la quebrada Aguada. 6°20'N, 77°20'W, 0-100 m. Epífita; flores amarillas, 30 Mayo 1990, **F. García C. & E.D. Aguilimpia 325* MO(3878341)! **CHOCO(not seen).** **WITHOUT LOCALITY:** No collection data: Climbing vine; sepals and petals pale yellowish-green; petals with flat ridge along center; lip white with crenulate, entire margins, inner throat with yellow and brown lines; column yellow; sweet, spicy fragrance. 6 May 1992, **S.W. Ingram 1421* SEL(066924)! same data **S.W. Ingram 1422* SEL(066925)!

5. *Vanilla hartii* Rolfe, Bull. Misc. Inform. Kew: 133. 1899.

TYPE: Trinidad, Cabasterre Arima, *Hart 6355*, holo. K!, iso. AMES(67785)!

V. leprieurii R. Port., Bull. Soc. Bot. France, 98: 94. 1951.

Type: "Guyane Française: Cayenne, dans les forêts humides, *Leprieur* (s.n.), en 1846" (not seen, drawing!)

COMMON NAMES: "Vanilla", "vainilla".

Hemiepiphytic vine, branching, leafy, relatively weak, up to 3 m high; perhaps up to 8-10 m long. **Stems** terete and smooth, green, 3-6 mm thick; internodes 7.0-12.4 cm long. Aerial, free **roots** terete, pale brownish, 8-12 mm long, 1-2 mm thick; attaching roots up to 6 cm long, 2 mm wide, conspicuously flattened. **Leaves** usually slightly shorter than the internodes; conspicuously petiolate, the petiole straight or twisted, canaliculate, with a clear junction line with the blade, ca. 10-14 mm long, 1.5-3 mm broad (not flattened); blades elliptic, acuminate, rounded at base, coriaceous, green, 9-11 nerved (and a similar number of smaller veins intercalated); 6.0-11.5 x 1.4-3.5 cm. **Inflorescence** a short raceme with about 5-8 flowers, 13-30 mm long, 3-3 mm thick; peduncle of 4-7 internodes; rachis 5-15 mm long. **Bracts** sessile, variable, triangular-ovate, acuminate to obtuse (the upper ones), concave (the upper ones) to cymbiform, not very stiff, progressively smaller, 3.5-9 x 2.5-5 mm. **Flowers** successive, 1-2 open at a time, segments spreading, ephemeral, but at least some of them remaining for more than one day, relatively small, tepals white, the sepals tinged with green, lip white with grayish or brown faint lines on the throat and an inconspicuous green cushion at lip apex; ca. 3.8 cm high; fragrance imperceptible. **Ovary** terete, green, smooth, 2.7 cm long, 1.2 mm thick. **Sepals** fused at base ca. 2 mm, subunguiculate and canaliculate at base, smooth. **Dorsal sepal** oblanceolate, apex acute, rounded, slightly thickened, flat to slightly concave, the apex slightly incurved, 12-veined, 39-49 x 6-8 mm. **Lateral sepals** obliquely oblanceolate, the lower margin more arcuate, apex obliquely subacute, rounded, thickened, slightly subcalyprate, and obscurely warty, 12-veined, 39-46 x 7-8.6 mm. **Petals** obliquely oblanceolate, somewhat arcuate, the lower margin more straight, long attenuate at base, apex subacute to widely rounded, ca. 12-veined, smooth, slightly concave; with an axial, flattened keel on the abaxial surface, ending in a cylindrical, acute, attached process, 39-50 x 6-8 mm. **Lip** attached to the column margins ca. 24-26 mm, long tubular, trumpet-shaped, basally gibbous, with an abaxial longitudinal groove; when spread out 37-43 x 14-25 mm; the claw slightly

sigmoid, ca. 16 mm long, minutely papillose-pubescent; blade cymbiform, ca. 7 mm depth, subentire or entire, constricted near the apex and appearing slightly trilobed, the apex deflexed, obovate-flabellate, ca. 21-veined, basal half with inconspicuous rows of papillae up to the penicillate callus, distal part with thickened veins, inconspicuously papillose, the axial ones more prominent and forming an apical inconspicuous cushion, margins denticulate-undulate, plicate, apex truncate; **penicillate callus** at 26-30 mm from the lip base; ca. 4 x 3 mm, built up by ca. 7 flabellate-praemorse, retrorse, lacerate-laciniate scales. **Column** very elongate and slender, semicylindric, 32-33 x 2-2.5 mm, apex dilated ca. 3-4 mm wide; slightly pubescent on the flat ventral surface, below the stigma, vertical wings flabellate-bilobed, with granulose inclusions, ca. 3 x 1.5 mm, filament broad, thick, ca. 1 mm long, 2 mm wide. **Anther** versatile, obovoid, ca. 3 x 2 mm. **Stigma** trilobed, the lobes emergent; with a flabellate rostellum, with the lateral margins reflexed, the margin denticulate, ca. 3.5 mm broad; lateral lobes emergent, ovate-quadrate, tongue-shaped, ca. 1 x 1 mm. **Fruit** linear-fusiform, elongate, cylindrical, not fleshy, slightly calyculated, dehiscent along 2 lines; fragrant, characteristic vanilla aroma, very sweet; 92-140 x 4-5 mm. Fig. 6, 16C.

DISTRIBUTION: Mexico (Chiapas, perhaps reaching eastern Oaxaca), Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Trinidad, Guyana, French Guiana, and probably Brazil.

ECOLOGY: Rare in wet forests at low altitudes, usually growing on understory treelets, in deep shade. Flowering time January to April. The Mexican population of *V. hartii* is sympatric with *V. cribbiana*, *V. insignis*, *V. odorata*, *V. planifolia*, and *V. inodora*, but *V. hartii* is confined to the top of small hills with shorter forests and open understory with tree ferns and large sedges; the other vanillas are absent from this habitat although they may be found a few meters away. Female *Euglossa* bees have been observed visiting the flowers, but we do not know if they are effective pollinators. *Vanilla hartii* is a shy flower-producer; we have visited over many years the Mexican population during the flowering season, and we have found open flowers only twice, in the spring of 2000, and then in spring of 2002.

This species was first cited from Central America by Correll (1965). The Central American material of *V.*

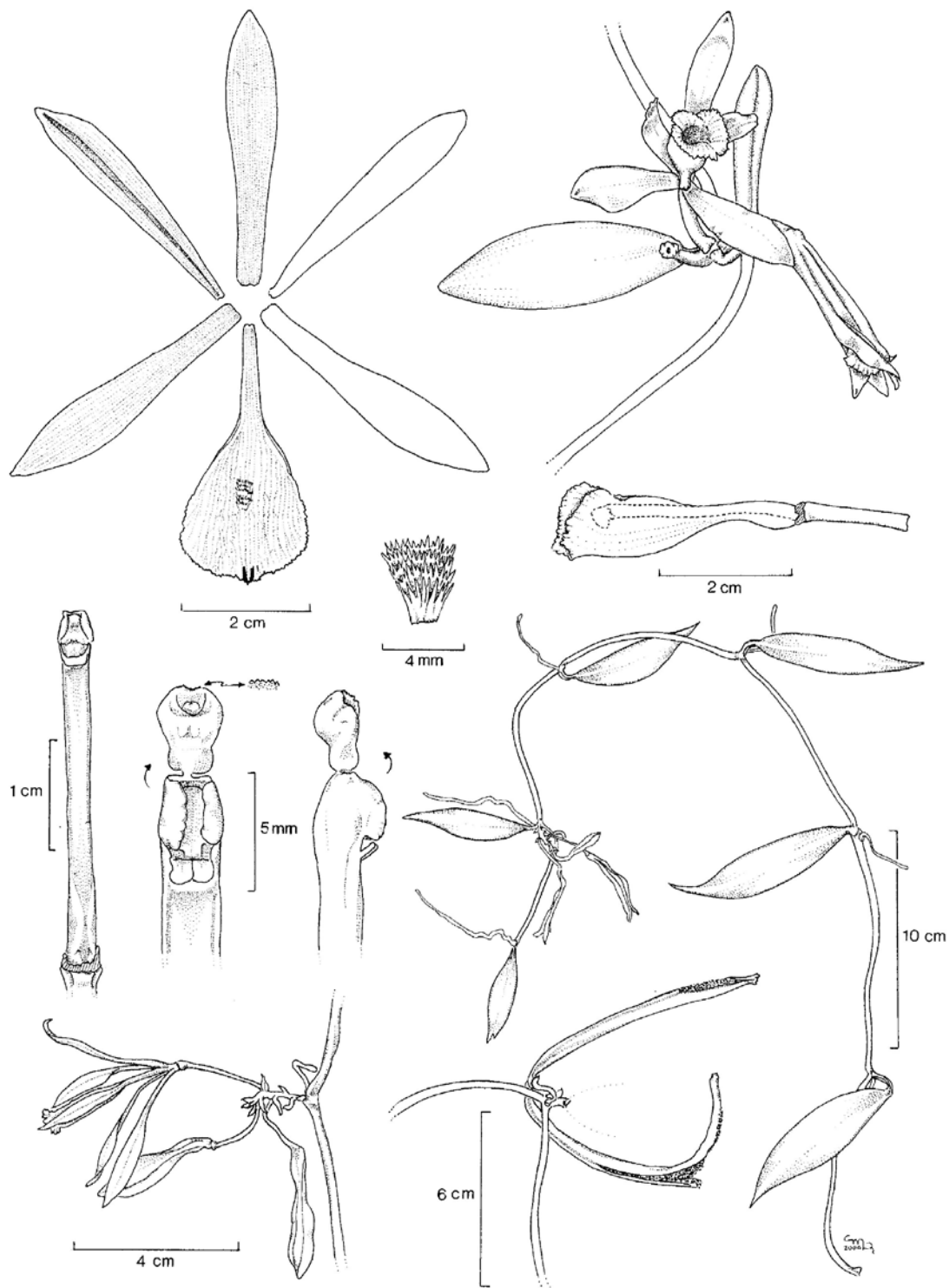


FIGURE 6. *Vanilla hartii* Rolfe, based on *M. Soto* 9729-9731. Drawing by M. López.

hartii has slightly larger flowers (e.g., lip is 37-43 vs. 32 mm long) and the lip apex was described originally as acute to subobtusate, not obtuse to widely rounded. However, examination of flower of the type and pictures from Trinidad and Mexico show that they are indistinguishable, and that the floral differences may be due to the herborization process. Three collections of *V. hartii* from the Pacific slope of Costa Rica are vegetatively stouter than Mexican and Trinidadian plants, and the flowers are also the largest examined. We do not know if these differences may indicate that they should be regarded as a distinct taxon; although molecular data suggest that they are closely related (see ITS analysis).

Vanilla leprieurii is here considered as a synonym of *V. hartii*. Portères (1954) stressed that his *V. leprieurii* was distinct because the nervation in the center of the lip was denser, with the zone before the nervation thicker, more imbricate scales in the penicillate callus, and the apex of the lip more emarginate, apiculate and pleated. Furthermore, the lip looks constricted, almost trilobed in the published drawing. All these features are variable in the material examined and again, they seem to be the result of the way in which the flowers were pressed.

Vanilla hartii is a relatively small vine similar to the *V. planifolia* group. It is somewhat similar to *V. odorata* but has shorter racemes, much smaller flowers, a gibbous lip base, subentire lip, denticulate-undulate (not lacerate-fimbriate) lip margin, a cushion-like thickening at the lip apex without retrorse papillae (vs. the 3-4 longitudinal rows of apical, retrorse, big papillae) and broader and shorter elliptic leaves (vs. long triangular-ensiform). The elliptic leaves, shorter than the internodes, and the slender stems make it vegetatively similar to *V. bicolor* from the Caribbean and Guyanas. However, *V. bicolor* has acute to subacuminate lip, larger, tan-colored flowers with yellow lip, and stouter, more elongate inflorescence.

Most Nicaraguan and several of the Central American specimens previously assigned to *V. planifolia* are actually *V. hartii*. Also the reports of wild *V. planifolia* from Rio Palenque Center in Ecuador are based apparently in *V. hartii* (P. Lubinsky, com. pers.).

Vanilla hartii is morphologically similar to *V. planifolia*, and even confused with it in many treatments. However, all the molecular data place it in

a rather basal position among the American penicillate vanillas. *Vanilla hartii* tolerates damper, more shady conditions, but the fragrant fruits are much smaller, and it is not a free-flowering plant.

OTHER RECORDS: **MEXICO:** CHIAPAS: Estación de Biología de Chajul, selva alta perennifolia, selva de loma con *Calophyllum* y sotobosque de cyperáceas altas y helechos arborescentes, sobre el camino a Arroyo Miranda, 16°07'35"N, 90°54'35"W; 200 m s.n.m., 12-IV-1997, *M. Soto* 8347 *AMO(sterile)! 8350 *AMO(fruit)! same data 14 abril 2000, *M. Soto* *9727(x2), *9729(x2), *S. Maldonado, L. López y P. Schlütter* AMO!; same data: flor blanca, tépalos algo más verdosos, especialmente en el engrosamiento apical, con líneas inconspicuas, café, tenues en la garganta, sin fragancia aparente. Rondada por *Euglossa* hembra, pero no capturada ni vista polinizando la flor. Fruto maduro con olor característico a vainilla, muy dulce *M. Soto* 9730, *S. Maldonado, L. López y P. Schlütter* *AMO! Sobre la Vereda La Granja, Estación de Biología de Chajul, selva alta perennifolia en zona de loma con muchos arroyos, algo perturbada, ca. 16°07'N, 90°54'W, 200 m s.n.m. escasa, en floración, 15 de abril de 2000, *M. Soto* 9731 y *P. Schlütter* *AMO! **BELIZE:** TOLEDO: "Vainilla" Vine, flowers white, in broken Cohune Ridge, between Orange Point and Moho River, April 28 1952, *P.H. Gentle* 7673 MEXU(511492)! Southern Maya Mountains, Bladen Nature Reserve, mountain, 1.7 airline north of Ex Xux archeological site, 16°31'05"N, 88°54'11"W, 500-600 m, vine, flower white, in tree fall gap, 24 May 1996, *G. Davidse* 36251 BM! COROZAL: [cf.] "vainilla", vine, *P.H. Gentle* 328 F(713628)! **GUATEMALA:** IZABAL: Leaves subcoriaceous, dark dull green above, slightly paler dull green below. Stem terete, dull green. Petals and sepals pale greenish-white. Lip white. Leaves somewhat narrower than in typical *V. fragrans*. Swamps of Salomón Creek, 1/2-1 mi. south of Bananera, alt. 50 m. April 6, 1940. *J.A. Steyermark* 38944 *F(1043051)! [cf.] Quebradas, 19-22, May 1919, *H. Pittier* 8589A NY(sterile)! *US(1013493; sterile)! **HONDURAS:** ATLANTIDA: [cf.], sterile Lancetilla Valley, near Tela, altitude 20 to 600 m; "vainilla", creeping on tree in wet forest; frequent, Dec. 6, 1927-Mar. 20, 1928, *P.C. Standley* 52824 *AMES(36946, fruit)! F(582560)! *US(1407340; sterile)! **NICARAGUA:** ZELAYA: Monkey Point; ca. 11°35'N, 83°39'W, elev 0-20 m; beach and bluff near village; vine on understory tree, flower pale green, 7 Apr 1981, *W.D. Stevens, B.A. Krukoff* 20021 *SEL(047700)! [cf.] Ibo, drainage of Caño Sung Sung, N of road between Puerto Cabezas and Río Wawa; approximately 14°9-11'N, 83°29-31'W, elev. less than 10 m; gallery forest and adjacent savanna. Vine on tree trunk, sterile. *W.D. Stevens & B.A. Krukoff* 10667 SEL(036668)! [cf.] Caño Zamora on Río Rama; ca. 11°57'N, 84°16'W,

elev. ca. 10 m; gallery forest along caño, pasture land on plain. Epiphytic vine, sterile. *W.D. Stevens, B.A. Krukoff* 8835 *SEL(054718)! without data [the attached flower; leaf, comments and analytical drawing on envelope perhaps belong to *V. planifolia*] *A.H. Heller s.n.* *SEL(03849)! **COSTA RICA: PUNTARENAS:** Hilly slopes west of Villa Nueva and Río Naranjo. Evergreen rainforest formations on the seasonally dry Pacific slope. Elev. ca. 200 m; 9°28'N 84°28' W. Vine growing in partial shade 1 m up on stump. Greenish-white flowers. 10-12 Feb 1988, *W. Burger, K. Swagel & J. Gómez-Laurito* 12251 F(2009056)! Cantón de Osa, Aguabuena. Cuenca superior de Quebrada Aguabuena. 8°42'40"N 83°31'40"W, 200-400 m. Bejuco trepador colgante. Inflorescencia de brácteas verdes. Flor blanco verde, labelo blanco con mancha puntual, apical, verde, columna blanca, polinios amarillo blanco. 18 January 1991, *G. Herrera* 4846 INB! **MO SAN JOSE:** Río Savegre, aproximadamente 1 km antes de la entrada a la Finca La Gavilana, cerca de los límites del Parque Nacional Tapantí, selva lluviosa con *Anacardium*, ca. 200 n.s.n.m., trepadora, con cápsulas, relativamente muy robusta, *E. Salas 1 & M. Soto* INB! **HEREDIA:** Sarapiquí, Chilamate. Finca El Bejuco, S end of Cerros Sardinal (N of Río Sarapiquí). 10°27'N, 84°04'W, 60 m. Vine climbing in understory tree at edge of forest to 3-4 m (transplanted here from swampy area of primary forest nearby). Sepals and wing petals cream-white. Labellum pure white, gibbous at very base, constricted 1/4-1/3 towards apex, gibbous again (more prominently) in apical 3/4, slightly narrowed before rotate margin. Labellum with grayish lines within. 24 January 1987. *M. Grayanum* 7998 & *T. Ray* *MO(3593651)! **PANAMA: PANAMA:**cf.] Río Tecumen. Moist forest; herbaceous vine; scarce, January 3, 1924, *P.C. Standley* 29353 *AMES(31441; sterile)!

6. *Vanilla helleri* A.D.Hawkes, *Phytologia* 14(1): 34, 19-20. t. 13.1966.

TYPE: **NICARAGUA:** Dept. Chontales: 2 miles south of La Libertad on the road to Sto. Tomás, growing as a vine on a wild avocado (*Persea* sp.) tree, alt. 1900 feet, April 1962, *A.H. Heller* 7946, holo. AMES? (not located), iso., SEL (fragments and drawing)!

Hemiepiphytic vine, branching, leafy. **Stems** flexuous, terete to slightly subquadrate, sulcate, dark olive green, minutely and inconspicuously papillose-rugose in living condition; 5-10 mm thick; internodes up to 15 cm long, the apical stems conspicuously covered with glaucous wax. Attaching, aerial roots flattened, 1-3 mm wide. **Leaves** subpetiolate, the petiole 9-12

mm long, the blade oblong-elliptic to oblanceolate (perhaps also elliptic), fleshy, abruptly constricted towards the acuminate apex (acumen 10-15 mm), 12-15 x 2.5-4.5(-6) cm. **Inflorescence** a 12-20-flowered raceme, candelabrum-shaped, 4-10 cm long; peduncle 1-2 cm long. **Bracts** triangular-ovate, acute to obtuse, dark green, up to 9 x 8 mm. **Flowers** successive, 1 open at once, with partially spreading segments, ephemeral, showy, medium-size, sepals whitish, greenish at the apical half on the abaxial surface, petals whitish, lip bright yellow with orange appendages on the midlobe, column white; ca. 6 cm diameter. **Ovary** slender, subterete, white, apex green, 39-50 mm long, 3 mm thick. **Dorsal sepal** oblanceolate-elliptic, subacute-subobtusate, slightly concave, fleshy, slightly subcalyprate at apex, 11-veined, 40-42 x 11-14 mm. **Lateral sepals** obliquely elliptic, obtuse, slightly concave, fleshy, subcalyprate, 11-veined, 40-45 x 13-14 mm. **Petals** oblong-elliptic, oblique, subacute to obtuse, rounded, 11-13-veined, dorsally keeled, 40-47 x 11-13 mm. **Lip** attached to the column margins up to the stigmatic region, forming an inflated throat, cuneate, without a claw, the blade clearly trilobed, when spread out 35-40 x 30-33 mm; lateral lobes flabellate-obovate, rounded, margins entire to slightly repand with branched veins, ca. 5 mm wide at apex; midlobe subquadrate to transversely oblong, truncate, covered with retrorse, complanate, appendages up to 3 mm long, along the veins; disc with inconspicuous axial rows of minute warts, with abundant trichomes on the sides of the basal half; **penicillate callus** at 20-23 mm from the base, almost continuous with the axial warts and the apical appendages, a tuft of long lacinate, scales, much divided, ca. 5 x 5 mm. **Column** subclavate, rather short and thick, semicylindric, 28 x 4 mm, apex dilated ca. 5 mm wide; ventral surface with fine glandular hairs below the stigma; vertical wings subtriangular, subacute, filament broad, thick, ca. 1 mm long, 2 mm wide. **Stigma** trilobed, with a convex, flabellate midlobe, the margin entire, ca. 3.5 mm broad; lateral lobes emergent, quadrate, tongue-shaped, ca. 1 x 1 mm. **Anther** versatile, transversely ellipsoid, ca. 3 x 3 mm. Fig. 7.

DISTRIBUTION: Costa Rica and Nicaragua, and also apparently in Oaxaca, Mexico. Our knowledge of the distribution of *V. helleri* is very fragmentary. It is known from the type locality on the slopes of the

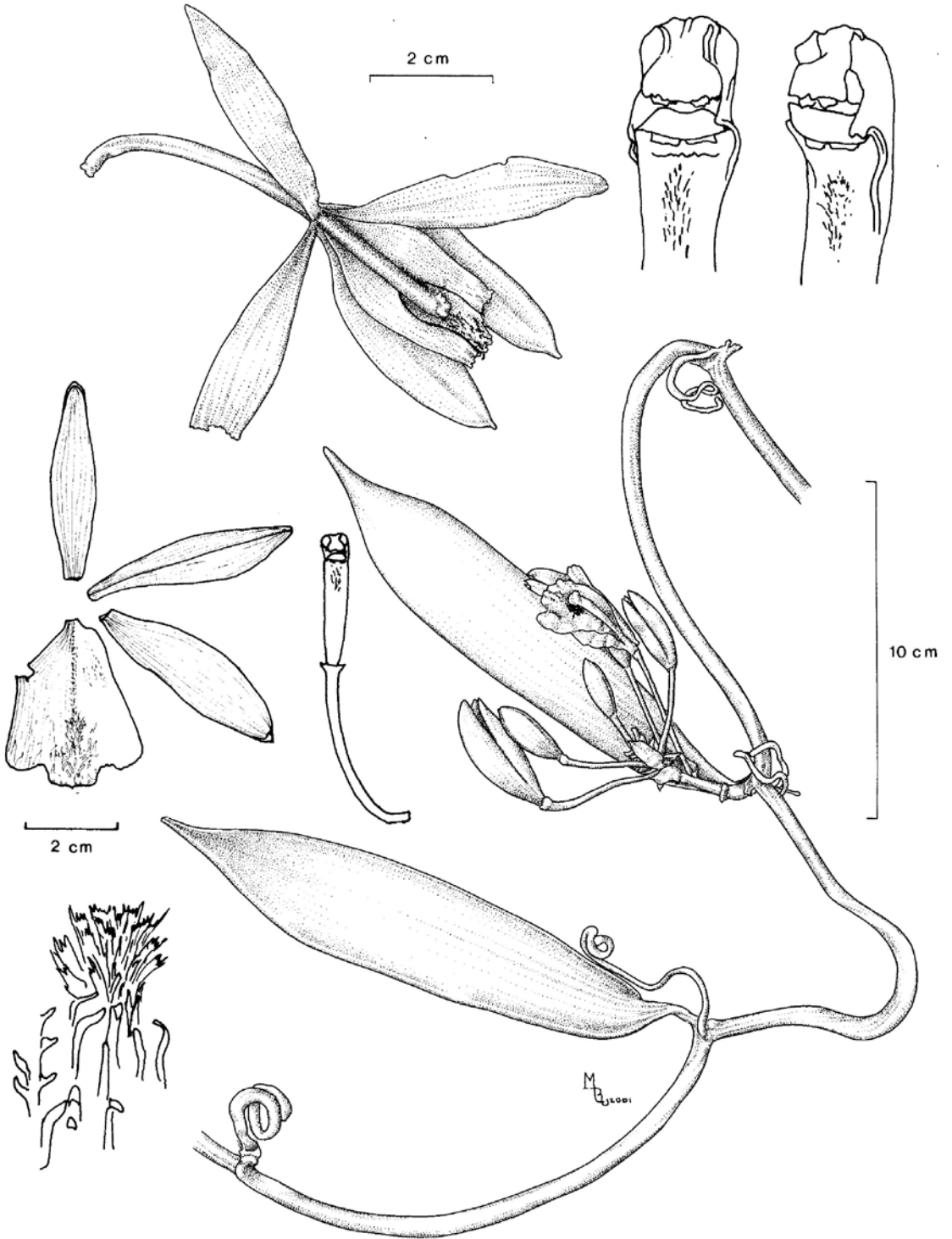


FIGURE 7. *Vanilla helleri* Hawkes. Based on G. Davidse & R.W. Pohl 1503. Drawing by M. López and M. Soto.

Cordillera Chontaleña, and on the Pacific slopes of S Costa Rica, especially in the Osa Peninsula.

ECOLOGY: In rainforest, with a short, marked dry season, at 200-570 m altitude; it flowers in March-April.

This species has a lip with elongate, complanate appendages, similar to that found in *V. insignis*. The outline of the lip, with a cuneate base lacking a claw is very anomalous among American penicillate vanillas and is reminiscent of some Old World species. In the original description Hawkes stressed that this species has no close allies in Central America. However, morphological and molecular data suggest that it is closely related to *V. insignis* and *V. odorata*, but the flowers are much smaller, and both these species have conspicuously long-clawed lip. *Vanilla helleri*, described 30 years ago is one of the rarest vanilla in the area; it is known only from a couple of flowering herbarium specimens. Despite its rarity in the herbaria, *V. helleri* could be more common than usually thought. Several specimens of it are growing at Finca La Gavilana, Río Savegre, Costa Rica. Additionally, several non-flowering plants, that may be this species, have been located around Sta. María Chimalapa, in Oaxaca, Mexico. Most Mexican specimens have rather elliptic, broader leaves than Costa Rican material, but they share the sulcate stems, papillose stem surface, abundant wax on stem apex, and the nucleotidic sequences are very similar to those of Costa Rica. Originally, the Mexican specimens were thought to be a hybrid between *V. planifolia* and *V. insignis*, since *V. helleri* has vegetative traits intermediate between these species. We hope to see their flowers some day.

OTHER RECORDS: **COSTA RICA:** PUNTARENAS: 2 km SW of the intersection of the Río Ceibo and Carretera Interamericana; elev. 200 m. Large vine climbing in a tree. 18 March 1969, *G. Davidse 1503 & R.W. Pohl* F(1731785)! **MEXICO:** OAXACA: [cf.] Planta joven, silvestre, en selva alta perennifolia con *Sebastiania*, *Quercus oleides*, *Terminalia*, *Acacia*, *Ampelocera*, ca. km 42 del camino Mezquite- Sta. María Chimalapa, 390 m s.n.m., 20 Marzo 1997, *A. Cibrián 11 & M. Soto* (not preserved). [cf.] Tallos ásperos al tacto y subpapilosos, longitudinalmente sulcados; al sureste de Sta. María Chimalapa, vereda hacia el Río Milagro, paso Quetz Tug, 15/XI/98 a 6/XII/98, *H. Hernández V7 sub M. Soto 8806* AMO(sterile, photo)! [cf.] Hojas subcuneadas en la base, algo oblancoeladas y algo oblicuas; 3 km al este de Sta. María Chimalapa, cerca de la

cascada Arroyo Sangre. 15/XI/98 a 6/XII/98 *H. Hernández V3 sub M. Soto 8811* AMO(sterile, photo)! [cf.] Tallos muy delgados, sulcados, ásperos, algo glaucos, hojas elípticas, flexibles y delgadas. Aproximadamente a 12 km al suroeste de Sta. María Chimalapa, a la orilla del camino Sta. María-El Mezquite, en la bajada de Zacatal, 15/XI/98 a 6/XII/98, *H. Hernández V8 sub M. Soto 8817* AMO(sterile, photo)! Tallos muy delgados, sulcados, ásperos, hojas elípticas, flexibles y delgadas. Aproximadamente 1 km al noreste de Sta María Chimalapa, a 5 m de la vereda de Paso Lagarto. *H. Hernández V2 sub M. Soto 8818* AMO (sterile, photo, ITS sequence)!

REFERENCES: Hamer, Orch. Nicaragua, Ic. Pl. Trop. pl. 1192. 1984; Hamer, *Selbyana* 11. Orch. Centr. A. p. 847. 1990.

7. *Vanilla inodora* Schiede, Linnaea 4(4): 574-575. 1829.

TYPE (?): “Baynilla de puerco Misantlensium”; Mexico, Misantla. *Schiede 1044*, K; “fruto inodori, Vanilla inodora nob. interin Vaynilla de puerco, Misantlensis Misantla, Mart 29 *Schiede & BM!* W(s.n.; x2)!

Vanilla pfaviana Rchb.f., Gard. Chron. 2, 20. 230. 1883.

Holotype: “Mexico” actually from Chiriquí, Costa Rica, *R. Pfau [269]* W(19347)!

Vanilla preussii Krnzl., Notizbl. Bot. Gart. Berlin-Dahlem. 7: 320. 1919.

Type: Bei der Pflanzung El Baúl im Buschwald, Heisst bei den Eingeborenen “Vainilla silvestre” (*Preuss n. 1445*), not seen.

COMMON NAMES: “Vainilla de puerco” (Ver.); “vainilla”, “vainilla cerro amarillo” (Oaxaca).

Hemiepiphytic herb, vigorous, up to 12 m high. **Stems** terete, ca. 4-5 mm thick; internodes ca. 7.5 long. **Leaves** usually hanging and with bending blades; petiolate, the petiole ca. 1-2 cm long, twisted; blades elliptic to broadly elliptic, abruptly acuminate, thin, membranaceous when dry; 12-21 x 4.5-7 cm. **Inflorescence** similar to the vegetative shoots; ca. 30 cm long, bearing 3-5 flowers; the raceme bears progressively smaller foliaceous bracts. **Bracts** similar to the leaves, although smaller or much smaller, 3.3-12 x 1.0-5.2 cm; the internodes 3.5-7 cm long, ca. 2 mm thick. **Flowers** resupinate, with spreading segments, very showy, tepals apple-green or

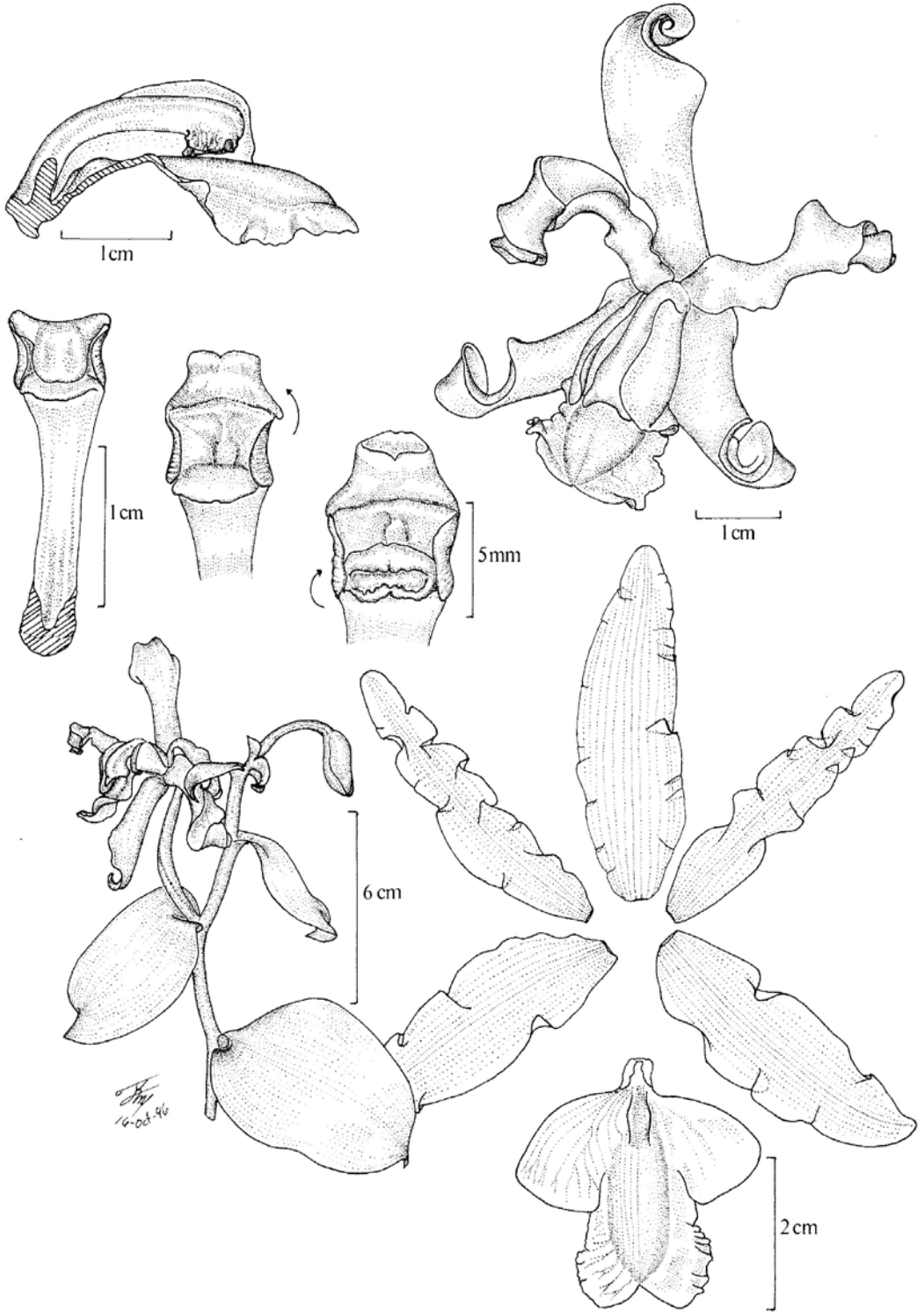


FIGURE 8. *Vanilla inodora* Schiede, based on *M. Hernandez s.n. sub M. Soto 7864*. Drawing by R. Jiménez.

yellowish green, shiny, lip white with yellow-orange tinge in the throat; ca. 4.5-5 cm diameter; fragrance sweet strong or faint medicinal, to weak solanaceous alkaloids; flowers lasting 2-3 days. **Ovary** straight to slightly arcuate, terete, smooth, 3-sulcate, the grooves twisted, 47-55 (48.67 ± 1.25) mm long, 3-4 (3.33 ± 0.47) mm thick. **Tepals** contorted, with very undulate, somewhat revolute margins, and the apices recurved or rolled backwards. **Dorsal sepal** erect, elliptic-lanceolate, broadly obtuse to acute, ca. 11-veined, 44-50 (47 ± 2.19) x 12-18 (13.4 ± 2.8) mm. **Lateral sepals** descending, elliptic-lanceolate, broadly obtuse to acute, ca. 11-veined, 41-44 (42.4 ± 1.02) x 13-17 (15.1 ± 1.79) mm. **Petals** spreading, elliptic-lanceolate, attenuate towards the obtuse apex, axially canaliculate on the abaxial surface, ca. 9-veined, 43-47 (45 ± 1.67) x 9-11 (10 ± 1.26) mm. **Lip** attached to the column ca. 2.5 mm at base; arcuate, trilobed, the lateral lobes covering the column, the midlobe spreading and deflexed; 27-36 (33 ± 3.16) mm long, 29-34 (31.6 ± 1.62) mm wide when spread out; lateral lobes erect, semiobcordate, broadly rounded, reduplicated and covering the distal half of the column; 20-24.5 (22.7 ± 2.23) x 9-13.5 (12.2 ± 1.69) mm; midlobe subcuadrate, spreading, deeply emarginate, the margins undulate, 12-17 (14.8 ± 1.94) x 13-19.5 (15.8 ± 2.38) mm; the midlobe and part of the disc with a massive, fleshy, elevated, cushion-like callus, 16-21 (18 ± 1.79) mm long, 5-8 (6.8 ± 1.16) mm broad, ca. 3-5 mm high. **Column** strongly arcuate, the apical part resting on the callus surface, 21-24 (22.6 ± 1.16) mm long, 5-6.3 (5.76 ± 0.56) mm wide at the apex. **Stigma** a well-defined, transversely oblong-panduriform cavity with thickened, yellow borders; without a rostellum. **Anther** hinge-like, broad, attached to the clinandrium, and forming together with it, a couple of lateral auricles. **Pollen** soft, somewhat sticky. **Fruit** cylindrical with attenuate base and apex, not aromatic, 18 cm long, ca. 8 mm thick. Fig. 8.

DISTRIBUTION: Mexico (Puebla, Veracruz, Jalisco, Guerrero, Oaxaca, Chiapas), Belize, Guatemala, Nicaragua (Heller & Hawkes, 1966), Costa Rica, and Panama.

ECOLOGY: *Vanilla inodora* grows in wet forests from 150 to 1600 m altitude; it is the only *Vanilla* that inhabits the cloud forests of the area, and is found in the lowlands only in sites with more than 2500 mm of rainfall. Flowering apparently without a defined

period. It is sometimes found in savanas with slow drainage.

Vanilla growers believe that this species can be self-pollinated; the large fruit set in some populations supports this idea; however, other populations have a fruit set as low as 2.5 %. The flowers remain in good condition for 2-3 days, and are therefore long-lived compared with other vanillas; often older and younger flowers are at anthesis on the same raceme.

The flowers of this vanilla resemble those of some species of *Schomburgkia* group of *Laelia* in the flower structure; the tepals are contorted, strongly twisted, with a varnished appearance and the column lies on the lip surface; pollination must be carried out by large, strong bees that try to enter to the throat separating the lip from the column, as in *Schomburgkia* or *Barkeria*; in the latter this work is done by carpenter bees (*Xylocopa*), and they might be good candidates to pollinate this species. We have observed carpenter bees approaching *V. inodora* in Chiapas, but they were not been seen landing on the flower.

V. inodora was collected by Schiede near Misantla; the original collections are housed at K, BM and W. None of the herbarium specimens bear flowers, although probably some specimens have had fruits (see Rolfe 1896); so its identity has been somewhat obscure. The type specimen is evidently a member of Portère's subsect. *Membranacea*, and as only a single species of this group is found in Mexico, and it is common in Veracruz, we discard the possibility of other species, from elsewhere, to which the name *V. inodora* has been applied. There is no evidence that the Mexican species is conspecific with the Haitian *Vanilla mexicana*, as suggested by many authors, despite the specific name of the latter. The large foliaceous bracts of *V. inodora* are larger than in other Membranaceous species and are clearly visible in the type.

Vanilla inodora has been known in recent years in the region as *V. pfaviana* Rchb.f. In their Orchids of Guatemala, Ames and Correll (1952) mentioned that they had not examined Guatemalan material of *V. inodora* and that the species could be conspecific with *V. pfaviana*. It seems, however, that the sterile specimens (or those very badly preserved) of this species were always identified as *V. mexicana* or *V. inodora*, while the material with flowers was thought to be *V. pfaviana*. *Vanilla inodora* and *V. mexicana*

are similar, but the massive, elevated, fleshy callus of *V. inodora* is very different from the 3-keeled callus found in *V. mexicana*; furthermore, *V. mexicana* can have much larger leaves. It should be noticed that the callus of *V. inodora* may appear to be keeled in old, withering flowers or in young buds.

The type of *V. preussii* Kraenzl. was destroyed in the Berlin bombing, but the description matches *V. inodora* very well. Furthermore, Schlechter, who must have examined the type specimen identified *Türckheim II 1764* as *V. preussii*.

The allied species in Central America are *V. martinezii*, from Guatemala, that is easily distinguished by the congested inflorescences, *V. costaricensis* with entire lip lacking a massive callus, and *V. sarapiquensis*, with short midlobe and a callus formed by two high, massive confluent ridges at the distal part of the lip. However, its closest relative may be the Andean *V. methonica* Rchb.f. & Warsz., with a similar, emarginate lip, but having 3 thickened and somewhat rugose keels instead the fleshy massive callus, and much smaller inflorescence bracts.

OTHER RECORDS: **MEXICO: JALISCO:** Steep mountainsides 3-10 km generally east on the road to Mina Cuale, from the junction 5 km northwest of El Tuito, Mpio. Cabo Corrientes; pine-oak forest on decomposed granitic soils, with *Podocarpus*, oaks, and other deciduous trees in rocky stream valleys, elev. 850-1150 m. Seen once, in rocky stream valley. Sterile; fleshy herbaceous vine climbing 10 m or more in trees, 16-19 February 1975, *R. McVaugh 26397* MEXU! Mpio. Cabo Corrientes, km 2.6 de la brecha hacia a la izquierda que sale del km 9.8 del camino El Tuito-Cuale, bosque de galería de *Hedyosmum*, *Inga*, *Podocarpus*, *Magnolia*, *Clusia*, en medio del bosque sabanoide de pinos y encinos, sobre granitos intemperizados, 900 m s.n.m., 20°22'29.4" y 105°15'21.9". Banco con suelo profundo con vegetación densa, similar a acahual de selva montana lluviosa con *Heliconias*, *Philodendrum tripartitum*, *Lindenia* y trepadoras. Hemiepífita, cerca 10 m de alto, con muchos frutos, cerca 400 m de extensión. Muy rara, sólo un espécimen visto. 27/junio/1998 *M. Soto 8626* y *E. Huerta* *AMO(x6)! **IBUG! GUERRERO:** System of Teotepec, near San Vicente, N.E. of Atoyac, in mixed oak-pine forest on tree trunks. 100°16'W, 17°17'N, 850 m, January 10, 1933. *O. Nagel sub E. Oestlund 1984* AMES (with sketch by B. Ames; 41396)! *AMES(51815)! *MO(11411617; sterile)!; San Vicente, north-east of Atoyac, towards Mt. Peineta. In mixed forest on trees & shrubs, 100°16'W, 17°17'N, ca. 100-1000 m, 10 Jan 1933. *O. Nagel sub E. Oestlund 1985* *AMES(41476, sterile)! BM(sterile)!

*MO(1145095; sterile)! **PUEBLA:** Vicinity of Puebla, Venant des sierras (De la décoration florale à l'archevêché) Déc. 8. 1907. *B.G. Arsène 1682* *AMES(71359, sterile)! *MO(843101, sterile)! NY! *US(1032010; fruit)! **VERACRUZ:** Miradores, 4/42 *Liebmann 297 K!* Mirador, *Liebmann W(11762)!* Hacienda de Java, 5/1841, *Liebmann 295/296 W(13537, 13538, 11761)!* Zacuapan, June 1919, *C.A. Purpus 8481* *AMES(71356)! NY! Region of Zacuapan, near Rancho Viejo, climbing on tree trunks, ca. 700 m, 10 Jul 1935, *C.A. Purpus sub E. Oestlund 4876* *AMES(sterile, 51843)! *US(1809800)! Near Zacuapan. On trees and shrubs, 12 Feb 1932, 96°52' W, 19°12' N, ca. 900 m, *O. Nagel sub E. Oestlund 2683* *AMES(sterile, 41475)! *US(1809491)! Region of Zacuapan, on tree trunks, 8 Oct 1935, ca. 800 m, *C.A. Purpus sub Oestlund 5045* *AMES(fruit, 51838)! Falda del Volcán de San Martín Tuxtla, San Andrés Tuxtla, 18°35', 95°09'W, alt. 800 m s.n.m., selva alta perennifolia primaria, suelo negro arenoso, buen drenaje, aluvial, cálido húmedo, lluvioso, escasa, flor blanca, 29-10-1973, *J.I. Calzada 01031* BM! **CHAPA! MEXU!** El Mirador, Mpio. Totutla, bosque de encino en cañada, 1000 m, herbácea trepadora, flor verde, centro blanco, fruto verde, escasa, 18-VI-1973, *F. Ventura 8417* *AMO(436)! **CHAPA! MEXU!** Lote 67, Estación de Biología Tropical Los Tuxtlas, 95°04' y 95°09' O, 18°34' y 18°36' N. Mpio. San Andrés Tuxtla, borde selva alta perennifolia, 300 m s.n.m, bejuco herbáceo, fruto verdigrisáceo, "vainilla", julio 14 de 1986, *S. Sinaca C. 835* *AMO(7066)! **OAXACA:** Cerro Martín, cerca de Usila, 400 m selva alta perennifolia, predio de Sebastián Arista, 22 mayo 1993, *M. Hernández s.n.* AMO(in spirit)! Usila, *M. Hernández s.n.* AMO(in spirit)! Usila, 2 mayo 1994, *M. Hernández s.n.* AMO(in spirit)! Cerro Martín, ca. Usila, 1992, *M. Hernández s.n.* AMO(in spirit)! La Escalera, Chinantla. "Vainilla Cerro Amarillo". abril-1990. *M. Hernández Apolinar sub M. Soto 10707* AMO! 1844, Mexico, *Karwinski M W(19347, sketch)!* Mpio. Sta. Ma. Chimalapa: Arroyo Sangre ca. 2 km E de Sta. Ma. Chimalapa, selva perturbada con *Calophyllum*, *Tapirira*, *Brosimum*, etc., suelo café parduzco con mucha hojarasca, 250 m, 16°54'30" 94°40", 20 abril 1985, bejuco, flor blanca, sépalos verde, aromática, en cañada, común, usos se pone en aceite para el cabello, *H. Hernández 1125* CHAPA! MEXU(564872)! Orquídea epífita, acahual derivado de selva alta perennifolia, loc.: Cuaje, Mpio. Ixtlán de Juárez, Dto. Ixtlán, Sierra Norte, 17/05/94, *E. Torres 367* AMO(16696; young fruit)! **TABASCO:** Hierba epífita como bejuco, flor con 5 tépalos semienriscados y una quilla blanca, inflorescencia con brácteas foliares, asociada a pukté en vegetación riparia, Teapa, 31-05-1990, *V. Ramón & A Sol 309* MEXU [sterile]! **CHIAPAS:** "Local name: "vainilla", in wet forest, Libertad Acacoyagua, June 1 1948, *E. Matuda 17912* AMES(66534; young fruit)! F(1616949)!

MEXU(85052)! En Crucero Corozal, camino Palenque-Boca Lacantún, Mpio. Ocosingo, 180 m s.n.m., bejuco con fruto, selva alta subperennifolia, 8 enero 1986, *E. Martínez 15730* *LL! MEXU(436979)! MO(4272282)! *XAL! Triunfo, Dec. 1936, *E. Matuda 360* *US(1689405)! Triunfo-Juárez, Escuintla, Dic. 1936, *E. Matuda 369* MEXU(85064)! Arroyo Miranda, entre los 6 y 20 km del arroyo partiendo del Río Chajul, Mpio. Ocosingo, 150 m s.n.m., primaria, orilla de arroyo, bejuco perenne, 8 m, flor blanca, nom. vul. “vainilla”, trepador, 20-02-1985, *G. Castillo et al. 4011* *XAL! 2 km al NW de Lacanjá-Chansayab; Mpio. de Ocosingo, 400 m, enredaderas; vainas verdes, lisas, negras cuando maduras; numerosas semillas negras cubiertas con una secreción pegajosa de las paredes internas de las vainas; abundante en remanente de selva alta perennifolia relativamente madura, abril 16, 1991, *M. González Espinosa et al. 1413* CHIP! MEXU(563979)! Bonampak, Mun. Ocosingo, 350 m s.n.m. selva alta perennifolia, suelo arcilloso. “Vainilla de montaña”. Enredadera muy escasa, hasta de 7 m de largo. abril 1982. *M. Soto 1020* AMO! Estación de Biología Chajul, Mpio. Ocosingo, ca. 200 m s.n.m., 16°08' N, 90°53' O. Cerca del Puente Hamaca en la vereda a la Sabana I. Loma con selva mediana-alta perennifolia, en la base de la loma. Muy escasa. 23 junio 1996. *M. Soto 7954-A* y *R. Solano* *AMO! km 223.6 de la carretera Palenque-Marquéz de Comillas, ca. de Benemérito de las Américas, selva mediana subperennifolia con *Cocoloba* y *Roupala*, 220 m s.n.m., 11-IV-1997, *M. Soto 8342 et al.* AMO(also in spirit)! Mpio de Ocosingo, ca. de las ruinas Los Sótanos-El Zapote, Estación de Biología de Chajul, selva alta perennifolia inundable con *Bactris*, 230 m, 16°08' N, 90°53' O. Sobre *Guarea* en sombra densa, con frutos. 12-IV-1997. *M. Soto 8343* *AMO! Estación de Biología de Chajul, junto al Río Lacantun, vereda La Granja, en la intersección con la vereda a La Sabana, selva alta perennifolia con *Ficus glabrata* en suelos profundos, arenosos, probablemente inundables estacionalmente, flor verde con labelo blanco, fragancia dulce, intensa, 15 de abril de 2000, *M. Soto 9726* & *P. Schlütter* *AMO!

BELIZE: **TOLEDO:** Gracie Rock, Sibun River, 1 May 1935, *P.H. Gentle 1672* *AMES(42338)! *LL! “Vainilla”. Climbing plant, on cohune tree, white flowers, in cohune ridge, near river beyond Columbia. January 31, 1947, *P.H. Gentle 6152* *F(1599314)! G! *LL(x3)! NY! *US(2572753)! “Vainilla”. Climbing vine, white flowers, in acahual, near Ocotol, Pine Ridge, 3 miles in trail from 7 Miles, Punta Gorda-San Antonio Road, January 20, 1950, *P. Gentle 6957* *LL(x3)! MEXU(511462)! *MO(3832518)! “Vianilla”, vine, in acahual, Feeders Road leading to Big Fall, April 13, 1950, *P.H. Gentle 7023* *LL(fruit, x2)! “Vianilla”, vine, in cohune ridge, one mile from 7 Miles, San Antonio-Punta Gorda Road, July 1, 1950, *P.H. Gentle 7078* *LL(sterile inflorescence, x 2)! “Vianilla”, vine, in cohune ridge, near

Columbia, August 15, 1950, *P.H. Gentle 7108* *LL(fruit)!

GUATEMALA: **IZABAL:** [cf., sterile] wet forest.. “Vainilla”. Creeping on tree trunk. Near Entre Ríos, alt. about 18 m., April 30, 1939, *P.C. Standley 72709* F(991636)!

ESCUINTLA: [cf., sterile] El Zapote, in jungle, on tree of *Ficus*, April 9, 1937, *W.C. Muescher 12480* F(905455)!

SAN MARCOS: [sterile] “vainilla”, climbing, leaves fleshy coriaceous, rich green above, practically same color but slightly paler beneath, above Finca El Porvenir on “Todos Santos Chiquitos”, lower south facing slopes of Volcán Tajumulco, alt. 1300-1500 m, March 7, 1940, *J.A. Steyermark 37076* F(1041850)!

HUEHUETENANGO: [cf.] Epiphyte, alt., At 3000 ft. alt. Cerro Chiblac, between San Rafael and Ixcán, Sierra de los Cuchumatanes, July 22, 1942, *J.A. Steyermark 49171* *AMES(63277, sterile)! F(1495682)!

SUCHITEPEQUEZ: [cf., sterile] Epiphyte on tree on bark, leaves fleshy subcoriaceous, dull dark green above, dull green beneath, stem pale green, in cafetal on opposite side of Finca, southern lower slopes of Volcán Zunil, vicinity of Finca Las Nubes, along Quebrada Chita, east of Pueblo Nuevo, alt. 500-800 m, Feb 2, 1940, *J.A. Steyermark 35412* F(1041244)!

BAJA VERAPAZ: Wald in Paujal, 1000 met April 1907, Bl. grün, Lippe weiss, *H. von Türckheim II 1764* *US(825825)!

HONDURAS: **COLON:** [cf.] Vine, flower white, Guaranta, Wispermini Camp, 75-100 ft., tropical rain forest, March 1938, *C. von Hagen & W. von Hagen 1352* F(942976)!

NY! **ATLANTIDA:** [cf.] banks of the Salado River, above the village of Salado ... on the mountain slopes and coastal plains, vicinity of La Ceiba, July 10, 1938, *T.G. Yuncker 8335* *AMES(fruit, 50661)!

NY! **COSTA RICA:** **ALAJUELA:** Reserva Biológica Monteverde. Río Aguas Gatas, Laguna de Arenal, El Castillo. 10°26' N 84°44' W, 600-1000 m. Epífita semi-liana dentro del bosque. Flor con caliz verde, corola blanca en forma de tubo. 11 August 1989, *E. Bello 1146* INB! [cf., without flowers] Reserva Forestal de San Ramón; camino entre el Río San Lorenzo y la estación. 10°12'53”N, 84°36'28”W. Epífita trepadora, frutos inmaduros verdes. *G. Herrera Ch., I. Chacón, D. Hernández, A. Solís y H. Gómez 386* SEL(062313)!

CARTAGO: vainilla, “Chiteria” = Chitaria, alt. 750 m, 15/4/36, *F. Solís* F(833816)! [cf., sterile]

LIMON: Epiphyte, 7 km al SW de Bribris, 100-250 m, May 4 1983 [sterile], *L.D. Gómez, R. Liesner, E. Judziewicz 20437* MEXU! MO [cf., sterile] San Clemente, Apr. 1920. *Lankester (k331)* K! **SAN JOSE:** Herbaceous vine, attached by roots. Fls green with white labellum, in forest. Vicinity of El General, alt. 1130 m, Feb. 1936, *A. Skutch 2592* AMES(*44231, *44232, *44233)! K! *MO(1105371)! NY! [Cataratas de San Ramón, marzo de 1931, *A.M. Brenes 13679* F(906350)!

PUNTARENAS: Cantón de Osa. Fila costeña. Río Piedras Blancas, cerca de la casa. Cerro Anguciana. Fila Cruces, 08°49'02”N, 83°11'23” W, 900 m. Bejuco trepador. Caliz verde, labelo

blanco. 10 December 1993. *R. Aguilar 2736* INB! **PANAMA: BOCAS DEL TORO:** [cf.] Vanilla, epiphyte; flower pale green, Big Bight, Vicinity of Chiriquí Lagoon, Oct., 27, 1940, *H. von Wedel 2880* *AMES(61513, sterile)! REFERENCES: Ames, Bot. Mus. Leaf. Harvard Univ. 4(3): 26-29. fig. p. 29. 1936.

8. *Vanilla insignis* Ames, Bot. Mus. Leaf. 2(8): 101-102. fig. p. 103. 1934.

TYPE: REPUBLIC OF HONDURAS, Dpt. Comayagua, Esquías, El Río Funes. Epiphyte in river-valley forest at 2,500 feet altitude. Sepals and petals green, lip white at base. April 27, 1933. *J.B. Edwards 407*, holo. AMES(40085)!; isotype AMES(40086)!

COMMON NAMES: "Sisbic" (Maya), "vainilla", "vainilla cimarrona" (Veracruz).

Hemiepiphytic, branching, leafy vine, usually very vigorous, up to 30 m high; up to a hundred meters long. **Stems** flexuose, subterete, with a conspicuous groove along the entire internode, surface fairly rugose-papillose, dark to olive green, ca. 6-9 mm thick; internodes, 10-17 cm long. Terrestrial **roots** pubescent, brown-whitish, ca. 2-3 mm thick; aerial free roots, terete, greenish gray, ca. 1 mm thick; aerial attaching roots semicylindric, flattened in the surface in contact with the substrate, ca. 3-4 mm wide. **Leaves** subpetiolate, petiole canaliculate, up to 11 mm long, 4 mm wide; blade oblong-elliptic, abruptly acuminate at the apex, rounded at base, coriaceous-fleshy, rather stiff, 4.2-19.5 x 1.5-3.4 cm. **Inflorescence** a 6-12(21)-flowered raceme, candelabrum-shaped, 4.4-11 cm long; peduncle fleshy, subterete, slightly compressed, 15-25 mm long, 6.5-8 mm thick; rachis 28-90 mm long, progressively slender towards the apex. **Bracts** sessile, small, broadly ovate, obtuse, concave, fleshy, progressively smaller towards the apex, commonly less than 9 x 6 mm, rarely up to 10 x 10 mm. **Flowers** successive, 1-3 open at once, ephemeral (from 8:00 to 14:00 hrs; starting to close at noon), very showy, segments completely spreading, tepals pale apple-green, shiny, lip cream-white with orange to dull yellow appendages on the midlobe, extreme apex green, penicillate callus cream, column white; ca. 11-12.4 cm wide, 9-11 cm high; fragrance weak, spicy. **Ovary** subterete, very slightly dorsiventrally

compressed, smooth, arcuate, 2-sulcate, the grooves almost straight, 45-54 (48.75±3.27) mm long, 4.5-5.5 (5±0.41) mm thick. **Dorsal sepal** long oblanceolate, apex acute, disatally rounded, slightly thickened, subcalyptrate, base attenuate-subunguiculate, claw ca. 22 x 11 mm, basally canaliculate, concave at middle, fairly incurved at apex, ca. 12-13-veined; 69-76.5 (73.16 ± 2.56) x 10.5-14 mm (11.6±1.24). **Lateral sepals** obliquely oblanceolate, the lower margin more arcuate, apex subacute, thickened, apiculate, subcalyptrate, smooth, the abaxial surface minutely warty, especially at the minute apicule, base attenuate-subunguiculate, basally canaliculate; slightly concave towards the apex, margins somewhat involute, ca. 11-14 veined, 64-74 (69.67±3.19) x 12.5-13.5 (12.92 ±0.35) mm. **Petals** obliquely linear to oblanceolate, somewhat arcuate, apex obtuse, distally rounded, oblique, subcalyptrate, base long attenuate; concave, with a very conspicuous, axial, elevated, flat keel at the abaxial surface, ending in a subtrigonal, free, adpressed process, ca. 2 mm long; ca. 12-14-veined, 68-74 (70.9±2.11) x 9-10 (9.76±0.39) mm. **Lip** fused to the column along the margins of the basal half (37-44 mm), long tubular, slightly concave, fairly inflated near the base of the blade; the apex conspicuously recurved-deflexed; axially grooved on the abaxial surface, the groove deep; when spread out 65-73 (69.33±2.49) x 30-35 (32.6±1.62) mm; long unguiculate, adaxial surface of claw hairy on the distal half, the trichomes dense, more or less in rows; ca. 26 x 7 mm; the blade approximately obovate-flabellate in outline, trilobed, ca. 30-veined, the veins branched above the middle, thickened forming low, obscure, flat keels near the base, disappearing near the basal third of the blade; lateral lobes subelliptic, oblique, ca. 33 x 10 mm, margins long laciniate-fimbriate, especially near the joint with the midlobe; cilia up to 7 mm long; midlobe ovate-suborbicular to oblong, obtuse, the margin undulate-crenulate to lacerate-dentate towards the lateral lobes, 11-15 (13±1.41) x 12.5-14 (13.37 ±0.65) mm; **penicillate callus** at ca. 34 mm from the base, 4 x 5 mm; made up by ca. 13 imbricated, retrorse, flabellate, praemorse to densely lacerate-laciniate scales, sometimes united to each other along the lateral margins, scales almost without adpressed processes on the surface, continuous towards the lip apex with 7 rows of tubercles, near of the base of the

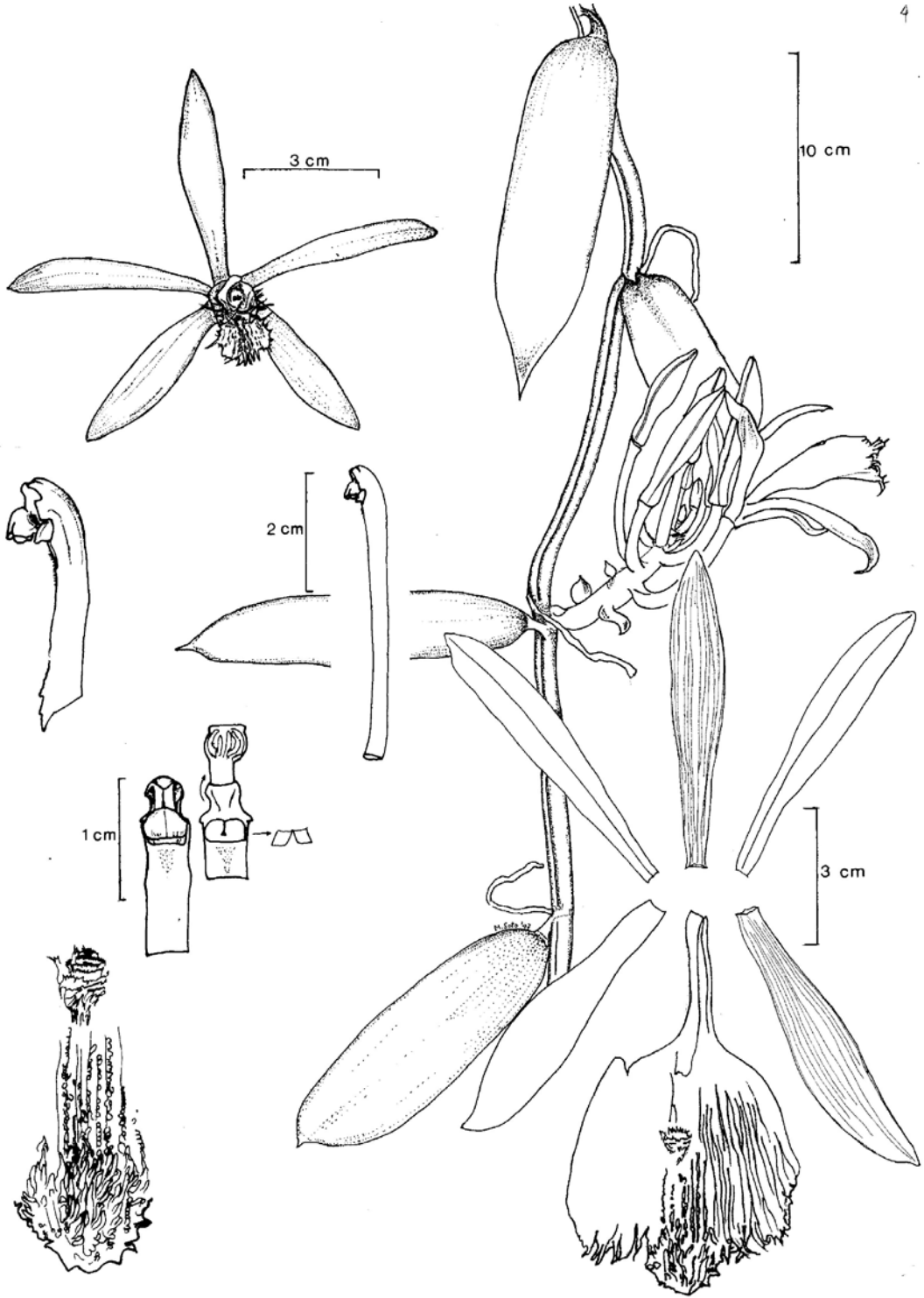


FIGURE 9. *Vanilla insignis* Ames. Based on *M. Soto* 7684. Drawing by *M. Soto*.

midlobe becoming enlarged to form conspicuous, retrorse, subtriangular, thick, complanate, sometimes conical, obtuse appendages, that cover almost entirely the surface of the midlobe, distributed approximately in 10 rows, the central appendages bigger, up to 4 mm long, 1 mm wide; extreme apex thickened, mound-shaped. **Column** very elongate and slender, semicylindric-trigonus, 49-52 (50.37±1.08) mm long, 4 mm wide; ventral surface flat, with scarce, minute trichomes below stigma; apex dilated, with vertical flabellate, somewhat trilobed wings, ca. 1.5 x 2.3 mm; clinandrium galeate, ovate, convex, 2 x 2 mm. **Stigma** trilobed, the lobes emergent, midlobe (rostellum) a transversely oblong, convex blade, axially grooved, ca. 3 x 4 mm, covering and parallel to the lateral lobes, these quadrate, rounded, convex, slightly divergent from each other, ca. 1.5 x 1.5 mm. **Anther** versatile, saddle-shaped, axially canaliculate, 3 mm wide, 1.8 mm thick, attached to the clinandrium margin by a thick, approximately semiterete filament. **Pollen** in monads, not forming a clear pollinarium but an ill-defined, sticky mass. **Fruit** short, thick, subclaviform-semifusiform, rounded, swollen towards the apex, green turning yellow when ripe, dehiscent along a single line, fragrant (less than *V. planifolia*), like a blend of common vanilla with coconut; ca. 7-14 cm long, 0.7-1.75 cm thick (n = 6). Fig. 9, 17C.

DISTRIBUTION: The Caribbean watershed of N Central America, in Honduras, Belize, Guatemala, and Mexico (Yucatán, Quintana Roo, Campeche, Chiapas, Tabasco, Oaxaca, and Veracruz; perhaps also in Puebla). Reported from Panama (Dressler, 1993) but the report seems to be based on specimens of *V. dressleri*.

ECOLOGY: From the level to ca. 900 m elevation. *Vanilla insignis* is probably the most common vanilla in Mexico (Soto Arenas, 2003), where it is widely distributed and forms large populations. It grows in dry and wet areas (1000 to 4000 mm of annual rainfall), but in the latter, is confined to savannas with especial edaphic conditions. It has been recorded only from calcareous substrates. In the Yucatan Peninsula it grows in the subdeciduous forests of *Bucida buceras*, *Brosimum alicastrum*, and *Manilkara sapota*, often with the understory dominated by the palm *Cryosophila argentea*; these areas have slow drainage during the rainy season, and are frequently associated to the flooded areas ("tintales") with *Haematoxylon*

campechianum. In the much moister areas of Chiapas, it is found in savannas with *Coccoloba belizensis*, *Quercus oleoides*, and *Roupala borealis*. In Central Veracruz *V. insignis* grows in tropical deciduous forest or in warm oak forest.

Some specimens in Campeche and Chiapas seem to occupy areas up to 4,000 m², and undoubtedly they are the largest plants of any *Vanilla* of the area. Some of these specimens may prove to be the most massive orchidaceous specimens in the world, with weights of many tons. It flowers in April and May; fruits become ripe in March-April. The flowers are visited by male bees of *Eulaema polychroma*.

This is another member of the *V. planifolia* complex and it has been considered conspecific with *V. planifolia* by some authors (e.g. Williams, 1956). However, it is clearly a distinct species; the flowers, though larger, are rather similar to those of *V. planifolia* in pressed specimens. The floral fragrance is also similar to that of *V. planifolia* (1-2-dimethyl-ciclopentane, ethyl acetate, and 1-8-cineol as principal constituents, although ocimene-trans is notoriously absent).

It is easily recognized because the stems have internodes conspicuously sulcate and their surface is fairly rugose-papillose. Similar vegetative traits are found in some very distantly related Asian species, namely *V. yersiniana* Guillaumin & de Sigaldi, *V. moonii* Thwaites, and its allies. The sulcate stems are thought to be an adaptation that permits the stem to store more water during the rainy period in seasonal areas, since the groove expands and becomes inconspicuous when the stem tissues are swollen. The characteristic flowers are large, ca. 11-12 cm in diameter, with green tepals, cream-white lip, the midlobe adorned with thick, triangular, retrorse projections, up to 4 mm high. The fruit (ca. 10-12 cm long) is thick and fragrant when ripe, but the aroma is similar to a mixture of vanilla with coconut.

The ITS tree (Fig. 1) and a survey of additional genomic regions, including also non-Mesoamerican *Vanilla* species show that the closest relatives of *V. insignis* are *V. odorata* Presl, *V. helleri* A.D.Hawkes, *V. uncinata* Huber ex Hoehne, and *V. tahitensis* J.W.Moore. *Vanilla odorata*, *V. uncinata*, and *V. tahitensis* have much narrower leaves, non-sulcate stems, smaller flowers, and less developed retrorse appendages on the lip. From *V. helleri*, from Oaxaca,

Nicaragua and Costa Rica, with which it shares the papillose stem surface, sulcate internodes, and long, retrorse, orange-coloured papillae on the distal part of the lip, it can be easily distinguished by the long claw of the lip found in *V. insignis* vs. the cuneate lip blade of *V. helleri*.

Vanilla insignis was described in 1934, and it is surprising that it has not been reported until recently from Mexico (Carnevali *et al.*, 2001; Soto Arenas, 2003) although it was collected in Veracruz by C.A. Purpus in 1919. Neither has it been reported so far from Guatemala or Belize, although a picture of *V. insignis* appeared wrongly identified as *V. pfaviana* in “Native Orchids of Belize” (McLeish *et al.*, 1995). However, this species has been known and used by the Mayas for a long time, who call it “sisbic”. Almost all the specimens previously identified as *V. planifolia* or *V. fragrans* from the Yucatan Peninsula and Veracruz belong to *V. insignis*. The report of *V. odorata* from Quintana Roo, based on *Cabrera 4611* (Soto Arenas, 1989) is based in a specimen with buds that is actually *V. insignis*.

Vanilla insignis, could add desirable features to the commercial vanillas; it also has fragrant fruits, it is a more xerophytic, stouter species, and apparently tolerates clayey soils, seasonally flooded in summer. We have cultivated this species and it is also the Mesoamerican species most tolerant to low and high temperatures, and much more resistant to the attack of pathogens than *V. planifolia*.

OTHER RECORDS: **MEXICO: VERACRUZ:** Zacuapan, June 1919, *C.A. Purpus 8482* *AMES(71362)! NY! Near Zacuapan, in humid forest on shrubs and on trees, 13 Feb 1932, 96°52' W, 19°12' N, ca. 900 m, *O. Nagel sub E. Oestlund 2682* AMES(*41478, *51844, sterile)! Region below Zacuapan, on shrubs, humid forest, 8 Jul 1936, ca. 800 m, *C.A. Purpus sub E. Oestlund 5961* *AMES(51845)! Near Zacuapan, in humid forest on shrubs, 15 Jun 1935, ca. 800 m, *C.A. Purpus 4866* AMES(*51849 fls. in spirit not seen, *51848, sterile)! Carretera Xalapa-Veracruz, km 16 SE of Xalapa, 1 km SE of main Jalapa-Huatusco highway, 5 km SW of bridge over Río Los Pescados, 5 km (by air) SE of Tuzamapan, Mpio. Coatepec, 19°21'N, 96° 50'W, 680 m alt., “selva baja caducifolia”, thorn scrub along now dry canyon, now very dry and most trees without leaves. Vine to 3 m, fruits green, hanging, March 19, 1983, *M. Nee & K. Taylor 26045* F(1985066)! *XAL! Mpio. Emiliano Zapata, Cerro de Chavarrillo, 19°26'N, 96°47'W, alt. 850 m s.n.m., selva baja, primaria, suelo arcilloso, pedregoso, color negro, muy seco, cálido, bejuco perenne, 6 m, escaso,

fruto verde; trepadora, 15-04-1979, *G. Castillo & L. Tapia 531* F(1963631)! NY! *XAL! Mpio. Emiliano Zapata, desviación de la carretera Xalapa-Veracruz, 16 km al SE de Xalapa, a 900 m de la carretera, enredadera, flor blanca y amarillo, escasa, “vainilla”, 23/V/1976, *C.H. Ramos 402* MEXU! [cf., fruits] Mpio. Soteapan, San Fernando, 18°17', 600 m, acahual, selva alta perennifolia, 2-3 m, “vainilla”, 19-IX-86, (usos) aromatizante de aceite, *M.C. González R. 303* *XAL! **OAXACA:** [cf., sterile] Forests ca. 25 km east of Mogoñé, near Río del Corte. On shrubs, rooting with long aerial roots in leafmould. Isthmus of Tehuantepec, ca. 94°57' W, 17°0' N, alt. ca. 100 m, 20 feb 1935, *O. Nagel sub E. Oestlund 4584* AMES(51847)! *US(1805098)! Plan Juan Martínez, camino Reforma-Ayozintepc, 80 m. Comprada al Sr. Eugenio Hilario Justo, quien la colectó expresamente para nosotros. 19-III-1997, *M. Soto 8120* y *A. Cibrián* *AMO(sterile)! **TABASCO:** [cf., sterile] Balancán, carretera no. 25, km 45 del entronque con la carretera E.W.O. hacia la carretera W-10, 10 m s.n.m. selva mediana subperennifolia primaria, asoc. *Manilkara sapota*, cálido húmedo, epífita, perenne, 5 m, escasa, nom. vul. “vainilla”, 06-12-1975, *P.E. Valdivia 2063* XAL! **CHIAPAS:** [cf., fruits] La Cueva, al NW del Rancho Corocito, Reserva del Ocote, Mpio. Ocozocuatlan. Alt. 770 m s.n.m., selva mediana perennifolia, primaria, suelo negro delgado con rocas calizas, ruderal, hierba, perenne, 3 m, escasa, fruto verde, nom. vul. vainilla, 29-04-1983, *J.I. Calzada, P. Gómez & B. Gómez 9695* *XAL! Mpio. Ocosingo, Estación de Biología de Chajul, Sabana I, a unos 3 km del Río Lacantúm, bosque sabanoide con *Roupala*, *Byrsonima*, *Scleria*, *Pteridium*, ca. 200 m s.n.m. 16°08' N, 90°53' O. 13-IV-1997, *M. Soto 8361* *AMO(buds)! **CAMPECHE:** Tuxpeña, Dec. 1, 1931, *C.L. Lundell 1070* F(700398)! Selvas medianas subperennifolias (*Manilkara-Chryosophila*) y bajos inundables, entre el Ejido 20 de Noviembre y las ruinas de Río Bec, Reserva de Calakmul, Campeche. Abundante, plantas más pequeñas que en Nueva Vida, sólo una vista con botones. Los mayas del ejido no la conocen. 11-IV-1995. *M. Soto, E. Martínez, G. Tavera, et al. 7656* *AMO! Reserva de Calakmul, cerca de Zoh Laguna, selva mediana subperennifolia con *Cryosophila argentea*, ca. 200 m altitud, 14 abril 1995, tépalos verdes, labelo crema con apéndices anaranjados, frutos aromáticos, fragancia a vainilla y coco, *M. Soto 7667* AMO(x2, also in spirit)! same data, [fruits], *M. Soto 7670* *AMO! Reserva de Calakmul, ca. de Nuevo Becar, en bajo, 13-IV-1995. *M. Soto 7681* *AMO! Ejido Nueva Vida, al N de Zoh Laguna, selva mediana subcaducifolia-subperennifolia de *Brosimum alicastrum*, *Protium copal*, *Platymiscium* sp., con mucha *Cryosophila argentea*, 230 m s.n.m.; planta vigorosa a la orilla del chilar; dos flores abiertas, 12.4 cm de diámetro, cerraron cerca de las 12:30; 3 *Eulaema* se aproximaron a las flores, no se posaron. Fragancia especiada, débil, no

identificada, 16-IV-1995, *M. Soto 7684* & *E. Martínez* *AMO! AMO(in spirit)! Ejido El Refugio, selva inundable de *Bucida buceras* a la orilla de la laguna, no la hay en el bajo de *Haematoxylon* contiguo. 230 m s.n.m., 17-IV-1995, *M. Soto 7685* & *E. Martínez* *AMO(x2)! 200 m, 18°35'N, 89°24'W, 1 Feb 1076, *P. Alvaro M & G. Bacao* 173 MO. QUINTANA ROO: Dense forest near shore of lagoon Chichankaná, on shrubs. N part of lagoon, 88°43'N, 19°52' W, ca. 50 m, 16 Aug 1935, *O. Nagel sub E. Oestlund 4973* *AMES(51850, sterile)! *MO(1145555; sterile) *US(1805110; sterile). Mpio. F. Carrillo Puerto, camino al Ejido X'konha', 4 m s.n.m., lat. 19°28'N, long. 88°03'W, selva mediana perennifolia primaria, cálido húmedo, suelo pedregoso de color negro con mucha materia orgánica, asoc. con árboles, es epífita, abundancia regular, bejuco, 10 m, perenne, tallo suculento, flor blanca, 8-V-1981, *J.S. Flores, E. Ucan 8236* CICY *XAL! En C. Vallarta, a 17 km al oeste de Puerto Morelos. Bejuco herbáceo con botones florales. Selva mediana con *Manilkara*, *Vitex* y *Thrinax*, 17 de abril de 1983, *E. Cabrera 4611* y *H. de Cabrera* *AMO! MEXU! [cf., sterile] A 16 km al S de la terminal del Ferry, cerca de la entrada a Palancar, selva baja a mediana con abundante *Lonchocarpus*, *Dalbergia* etc., suelos inundables, epífita sobre tronco, 22/Nov/1982, *E. Cabrera 9768*, *O. Téllez*, y *E. Linares* MEXU(421555)! La Pantera, 1997, *Carnevali s.n.* AMO(sterile)! YUCATAN: San Antonio, Rancho al sur de Pixoy, lat. 20°42'N, long. 88°14'W, alt. 22 m s.n.m., selva baja caducifolia, secundaria, en la orilla de una mensura, suelo moreno, pedregoso; abundancia regular, hierba, 6 m, perenne, fruto verde; obs. provoca comezón en la piel, 12-08-1983, *E. Ucan 2761* CICY *XAL(fruto)! Mpio. Valladolid, Ebtún cabecera rumbo a Pixoy, lat. 20°41'N, long. 88°14'W, alt. 22 m s.n.m., selva baja caducifolia, secundaria, en la orilla del camino, suelo moreno, abundancia regular, hierba, 6 m, perenne, flor verde amarilla, 11-05-1983, *E. Ucan 2463* *XAL! GUATEMALA: IZABAL: [sterile] climbing on dry pine slope; leaves coriaceous, dull green above, paler dull green beneath, stems dull olive-green, warty rugulose, with a sulcation on each side, between Milla 42.5 and ridge, 6 miles from Izabal, Montaña del Mico, 65-800 m altitude, April 1, 1949 *J.A. Steyermark 38539* F(1043863)! [cf., fruit] A 8 km al NO de El Estor, 210 m s.n.m., hierba trepadora con fruto, sabana, 30 agosto 1988, *E. Martínez 23348* & *D. Stevens* MEXU(480867)! MO(3656561)! Punta Palma, Sto. Tomás, 100 m de la entrada de la playa por el lado norte, 3 ó 4 plantas en la playa, 22 febrero 1998, *M. Dix sub M. Soto 8611* AMO! ALTA VERAPAZ: [cf., sterile] Climbing, stems terete, deep green, savanna north of Concepción, 3-5 miles southeast of Finca Yalpemech, near Alta Verapaz-Petén boundary line, alt. 100-110 m, March 23, 1942, *J.A. Steyermark 45233* *AMES(sterile, 63988)! F(1195510)! BAJA VERAPAZ: [cf.] Jocoló, climbing up trees, wild species of *Vanilla*, fruits said to be short, used as flavoring,

100 ft, Jan 30 1921, *H. Johnson 1178* AMES(22753, sterile, perhaps *V. cribbiana*)! PETEN: "Vainilla", fleshy vine, Tikal National Park, Bajo de Santa Fé, salida de Arroyo Corriental, in tinto on Aguada Términos road, March-June, 1959, *C.L. Lundell 15940* *LL(fruit)! same data *C.L. Lundell 15818* *LL(fruit)! BELIZE: COROZAL: Maskall, Dec. 1933, *P. Gentle 1063* *AMES(40496, sterile)! NY(fruit)! TOLEDO: "Vianilla", vine, in cohune ridge, Cañada Hill-Alta Vista Road, November 2, 1953, *P.H. Gentle 8054* *LL(fruit)! NICARAGUA: ZELAYA: Cerro Waylawas, 10 km south of Siuna; elev. 250 m. Vine; scrambling over rocks; leaves thick, fleshy (sterile). 5 June 1978. *D. Neill 4219* SE(049333)!

9. *Vanilla martiniezii* Soto Arenas, *sp. nov.*

TYPE: GUATEMALA: IZABAL: Mpio. Livingston, El Golfete, a 20.4 km al NE de Río Dulce por lancha camino a Calix, bejuco herbáceo, flor verde con amarillo y labelo blanco; selva mediana perennifolia 'swampo', 15°47'06"N, 88°51'42"W; *E. Martínez S. 36410* y *D. Alvarez*, holo. MEXU!, iso. AMO! BIGUA! MO!

Vanillae inodorae similis sed foliis membranaceis-chartaceis, inflorescentia brevis laxa quasi sub sessili, bracteis viridis non foliaceis, floribus majoribus, sepalis rectis, petalis undulatis, labello subintegro vel quinque lateribus, fere longo quam lato, carinis humilibus inconspicuis ornato.

Hemiepiphytic vine, leafy, up to 10 m high. **Stems** terete-subquadrate, somewhat keeled (in dried condition), ca. 2-4.5 mm thick; internodes 3.9-7 cm long. Aerial, free **roots** pale brownish, dorsiventrally compressed, 2-3.3 cm long, ca. 1 mm wide. **Leaves** petiolate, the petiole up to 16 mm long, canaliculate; blade elliptic, acuminate, base obtuse, somewhat conduplicate; membranaceous-chartaceous (in dried condition), 7.5-21 x 3.5-7 cm. **Inflorescence** strongly dissimilar to the vegetative shoots, 26-50 mm long, a short, lax, 4-6-flowered raceme (rarely branched at base), subsessile, the peduncle up to 13 mm long, the rachis zigzag, at least ca. 3 mm thick, flowers separated by 9-14 mm; with 1-2 peduncle bracts, clasping, ovate, concave, up to 10 x 7 mm. **Floral bracts** ovate, concave, obtuse to acute, apparently thin, 4-17 x 2-6 mm. **Flowers** successive, apparently 2 open at once, very showy, with rather spreading segments, tepals yellow green, lip white, ca. 5.5 cm high, 6.5 cm wide.

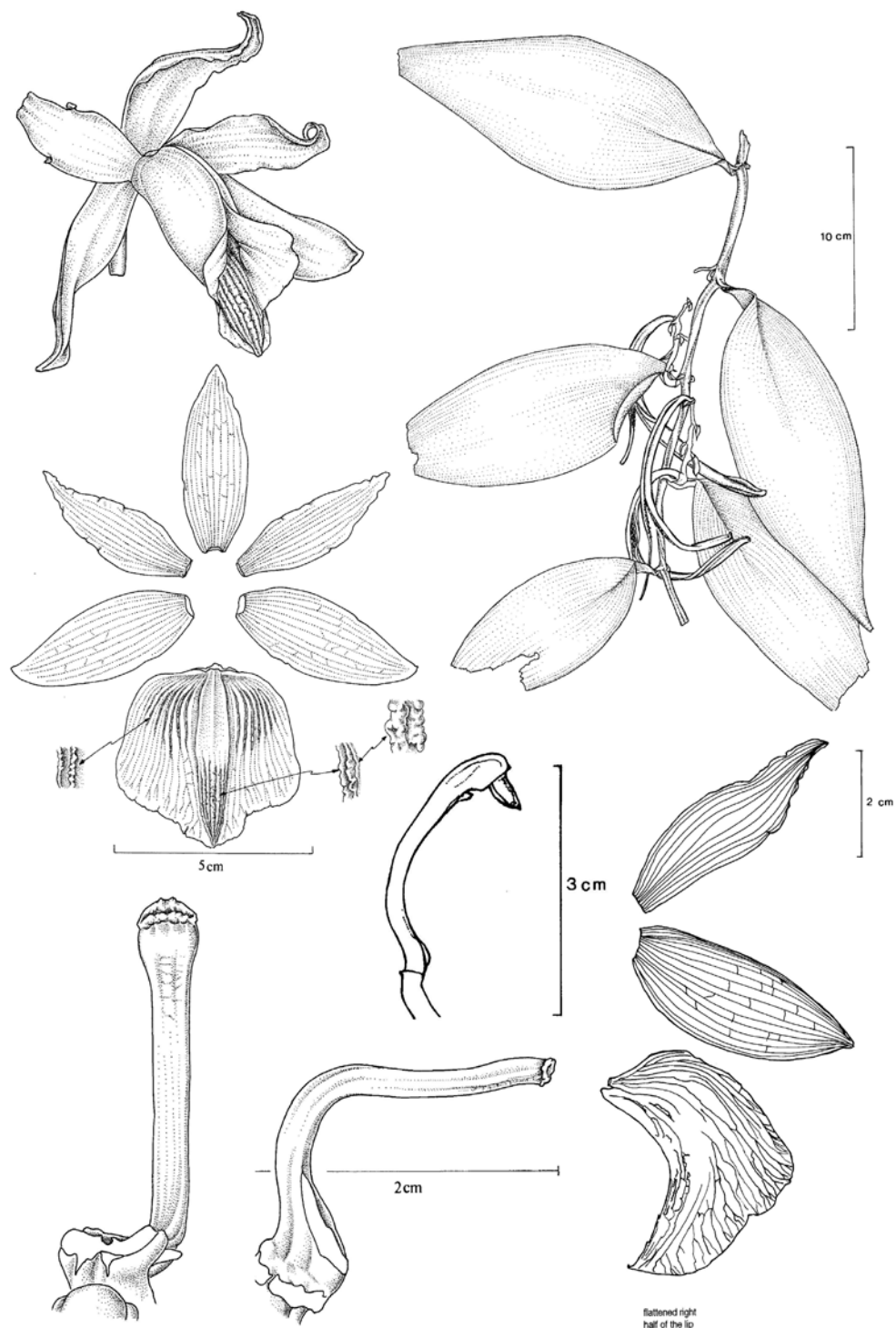


FIGURE 10. *Vanilla martinezii* Soto Arenas. Based on the type, *E. Martínez* 22790, and *M. Soto* 8602a. Drawing by M. López and M. Soto.

Ovary terete, smooth, arcuate to straight, 2-sulcate, the grooves almost straight, 52-53 mm long, 4 mm thick. **Dorsal sepal** lanceolate elliptic, apex acute, base obtuse, basally and apically grooved on the abaxial surface, obscurely and broadly keeled at the middle, margins thinner, somewhat reflexed and slightly undulate along its entire length, fleshy, incurved at apex, concave at middle, ca. 11-veined; 45 x 14.5 mm. **Lateral sepals** very slightly oblique, elliptic, the upper margin may be or not almost straight, acute to obtuse at apex, almost subcalyprate, slightly recurved and curved upwards; basally obtuse, slightly canaliculate-concave, broadly keeled on the abaxial surface, the keel narrower and higher at apex, smooth, margins thinner, minutely inflexed, almost entire and just slightly undulate, little pleated to straight, ca. 11-veined, 46-47 x 17-18 mm. **Petals** arcuate, obliquely elliptic to lanceolate, somewhat arcuate upwards, apex long acute-acuminate, recurved-rolled, base acute, subtruncate, conspicuously grooved all length of the abaxial surface, ca. 10 veined, margins undulate and pleated, especially near the apex, 43-47 x 11-13 mm. **Lip** fused basally to the column ca. 7 mm, arcuate, funnel-shaped, the lateral lobes-margins erect and forming a gullet around the column, the apical lobe-margin deflexed; impossible to flatten without some distortion, subentire-obscurely trilobed, trapezoidal-subpentagonal to suborbicular-subpentagonal, base truncate with widely rounded 'shoulders', apex truncate-rounded, minutely mucronate, appearing triangular in natural position, axially grooved on the abaxial surface; 42-44 x 44-47 mm, ca. 27-34-veined, veins branched above the middle; **callus** lip length, made up by a broad, 7 mm wide, flat, fleshy plate constructed by 3 obscure keels from the base to near the middle, progressively becoming ovate-triangular in cross section and then divided in ca. 11 low, sinuous, rugose-warty, inconspicuous keels reaching the apex as a narrow high, almost smooth keel; the lateral ca. 10 veins (on each side) slightly raised and minutely rugose-warty; lateral lobes-margins almost entire, and apparently somewhat reflexed, apical lobe margins slightly undulate-pleated. **Column** relatively short, strongly arcuate, the basal part forming a rather abrupt 60° angle with the apical part, semiclaviform, apex dilated, smooth, ca. 28 mm long (across de arch); vertical wings oblong, inconspicuous, 4.5 x 1 mm. **Anther** strongly attached to the clinandrium by a broad,

short filament, ovoid, ca. 4.5 long, 2 mm wide. **Stigma** a cavity, the midlobe concave, oblong, perpendicular to the column axis. **Fruit** clearly dehiscent, opening by 2 sutures, leaving unequal valves, 2-3 and 7-10 mm wide respectively, non-aromatic except by a resinous faint smell, dark brown, blackish inside, with ellipsoid seeds with slightly warty surface; 9.5-15 cm long, 6-8 mm thick before dehiscence. Fig. 10.

DISTRIBUTION: Known only from eastern Guatemala, but also to be expected from adjacent wet areas of Belize and Honduras. It may also be native to Mexico. DNA from a sterile specimen of a membranaceous *Vanilla* collected in Crucero Corozal, in the Selva Lacandona, Chiapas, Mexico, *A. Ibarra P. 2222?*, was sequenced (ITS, matK), and it shows a strong relationship to *V. martinezii*, yet it seems different from the sympatric *V. inodora*; we suppose that it belongs to *V. martinezii*, although its sequences are somewhat divergent from the Guatemalan material. This locality is known to have populations of very thermophilous plants, that are very rare in other rain forest areas of Mexico (e.g. *Lacandonia schismatica*, *Chysis limminghei*, *Warrea costaricensis*, *Ligeophila clavigera*, *Specklinia haberi*, *Maxillaria alba*); furthermore the substrates in this area are partially flooded and with peat-like soils.

ECOLOGY: In lowland, wet, swampy areas of high rainfall. Locally abundant. Flowering in February and July. As far as we know, this vine grows only on islets in the delta of the Polochic River into Lake Izabal and similar habitats near the coast in the area known as Golfete; its habitat could be very specific, since these islets have an unusual peat-like soil. In the only flower that we have examined, the midlobe of the stigma is perpendicular to the column body, and the anther is also protruding. The fruit set in *Vanilla martinezii* is very high (up to 53% in a clone) which suggests that it could be self-pollinated.

Vanilla martinezii is known only from two or three nearby localities. *Vanilla martinezii* is a species of the membranaceous group; which, together with *V. costaricensis*, *V. inodora*, and *V. sarapiquensis*, are the only members of this clade in Mesoamerica. It is different from other species by the following combination of characters: membranaceous-chartaceous leaves, short, lax, almost subsessile inflorescences (strongly different from the vegetative

shoots); short, non-foliaceous bracts, large flowers with straight sepals, undulate petals, and by the huge subentire to subpentagonal, free lip, about as long as wide, and with very low and inconspicuous axial keels. Both *V. costaricensis* and *V. inodora* have elongate inflorescences similar to their vegetative axes, and leaf-like bracts. *Vanilla inodora* is also easily distinguished by its cushion-like, axial callus and its emarginate lip; *V. costaricensis* is more similar to *V. martinezii*, but has smaller flowers, twisted-undulate sepals, and the lip surface is adorned with a rugose sculpturing, especially at the sides of the lip.

The most similar species is *V. guianensis* Splitgerber, from Guyanas and Amazonia (better known by its synonyms *V. acuta* Rolfe and *V. latisegmenta* Ames & Schweinf.). Both have membranaceous-chartaceous leaves, short, few-flowered inflorescences with small, non-foliaceous bracts, subentire lip which is strongly veined, and similar column morphology with basal wings. However, in *Vanilla martinezii* the axial keels of the callus are warty, numerous, and not well-defined at the apex, some of them extending to the basal, lateral sides of the lip and the latter is not as trilobed at apex; in *V. guianensis* the callus is formed by 5 basal keels and 3 rather prominent ones, but it is not or only scarcely verrucose, and the lip apex is trilobed.

Vanilla martinezii seems to be another endemism of the wet lowlands around Lake Izabal, a site which has been proposed as a primary refuge for a diverse tropical rain forest biota (Toledo, 1982; Wendt, 1989, 1993). Its affinities with the Amazonian *V. guianensis* make its distribution even more interesting.

OTHER RECORDS: **GUATEMALA: IZABAL:** Creek Lagarto, Ensenada de los Lagartos, El Estor, 2 m s.n.m., bejuco, flor blanca, selva mediana perennifolia inundable, 16 julio 1988, *E. Martínez* 22790, *P. Tenorio, H. Droege & M. Díaz* MEXU(480869)! Lago Izabal, desembocadura del Río Polochic, Creek Lagarto, al SW de El Estor, selva mediana inundable con *Pachira aquatica*, sobre suelos con mucha materia orgánica (peat), con *Epidendrum stamfordianum*, *E. flexuosum*, *E. cardiophilum*, *E. raniferum*, *Oncidium sphacelatum*, *O. luridum*, *Pleurothallis marginata*, *P. sertularioides*, *Maxillaria crassifolia*, *M. elatior*, *Gongora* aff. *quinquineris*, *Coryanthes picturata*, *Myrmecophylla brysiiana*, *Sobralia decora*; cerca del nivel del mar, ca. 15°28'N, 89°23'W; común, hasta de 10 m de alto; 24 febrero 1998, *M. Soto 8601a* AMO! mismos datos, 23 cápsulas de 43 flores, *M. Soto 8602a* AMO!

The next specimen from a nearby locality is sterile, but it matches *V. martinezii* in vegetative aspect; however it could be *V. inodora* Schiede, usually with broader leaves: IZABAL: Vicinity of Quiriguá; altitude 75 to 225 m, May 15-31, 1922, *P.C. Standley 24554*

10. *Vanilla odorata* C.Presl, Reliq. Haenk. 1: 101. 1827 [1830].

TYPE: [ECUADOR:] Hab. in Guayaquil, *Haenke*, holo. PR(305753)! iso. (x2; 305751,305752) [all sterile and mounted with fragments of a *Dimerandra* species].

V. ensifolia Rolfe, Kew Bull. 1892, p. 141.

Syntypes: [COLOMBIA:] Cauca, Peñol, Aout, *Goudot*, K! [with a drawing of the other syntype, "Leaves, flowers & seed of Vanilla -- Patia, presented by Mr. J. Hanbury 1884" Herb. Pharmaceut. Soc.]; P(flowers poorly preserved)!

Epidendrum vermifugum Sessé & Moc., Fl. Mex. ed. 2: 201. 1894.

Lectotype: (Soto Arenas, 1994): "Epidendrum vermifugum, *Sessé, Mociño, Castillo & Maldonado (4358)* MA [sterile]!; isolectotype "Epidendrum vermifugum de México absque foliis" [only floral buds, mounted with "Epidendrum uniflorum"], BM! F(848611)!

COMMON NAMES: "vainilla Tlatepusco" (Usila, Oax.); "Vainilla de Teutila", Humboldt.

Hemiepiphytic vine, branching, leafy, up to 6 m high. **Stems** flexuose, terete, smooth, dark green, with whitish dots, 4-6 mm thick; internodes 7-10.5 cm long. Terrestrial **roots** conspicuously pubescent; aerial, free roots terete, green to pale green, 1 mm thick; attaching, aerial roots strongly flattened. **Leaves** subsessile; the blade lanceolate to ensiform, very narrow, sometimes oblique, acuminate to long acuminate at apex, very dark green on both surfaces, 8-13 x 1.5-2.7 cm; ca. 1.8 mm thick in fresh. **Inflorescence** a 6-12-flowered raceme, rachis 30 mm long, 6 mm thick. **Bracts** subsessile, concave, membranaceous, subsessile, progressively smaller, ca. 8 x 5 mm. **Flowers** successive, 1-2 open at once, with spreading segments, ephemeral (from 7:00 to 16:00 hrs), showy, tepals whitish green, translucent, lip greenish white, the throat striped with pale yellow lines, callus white, column white; ca. 8 cm high, 7 cm wide;

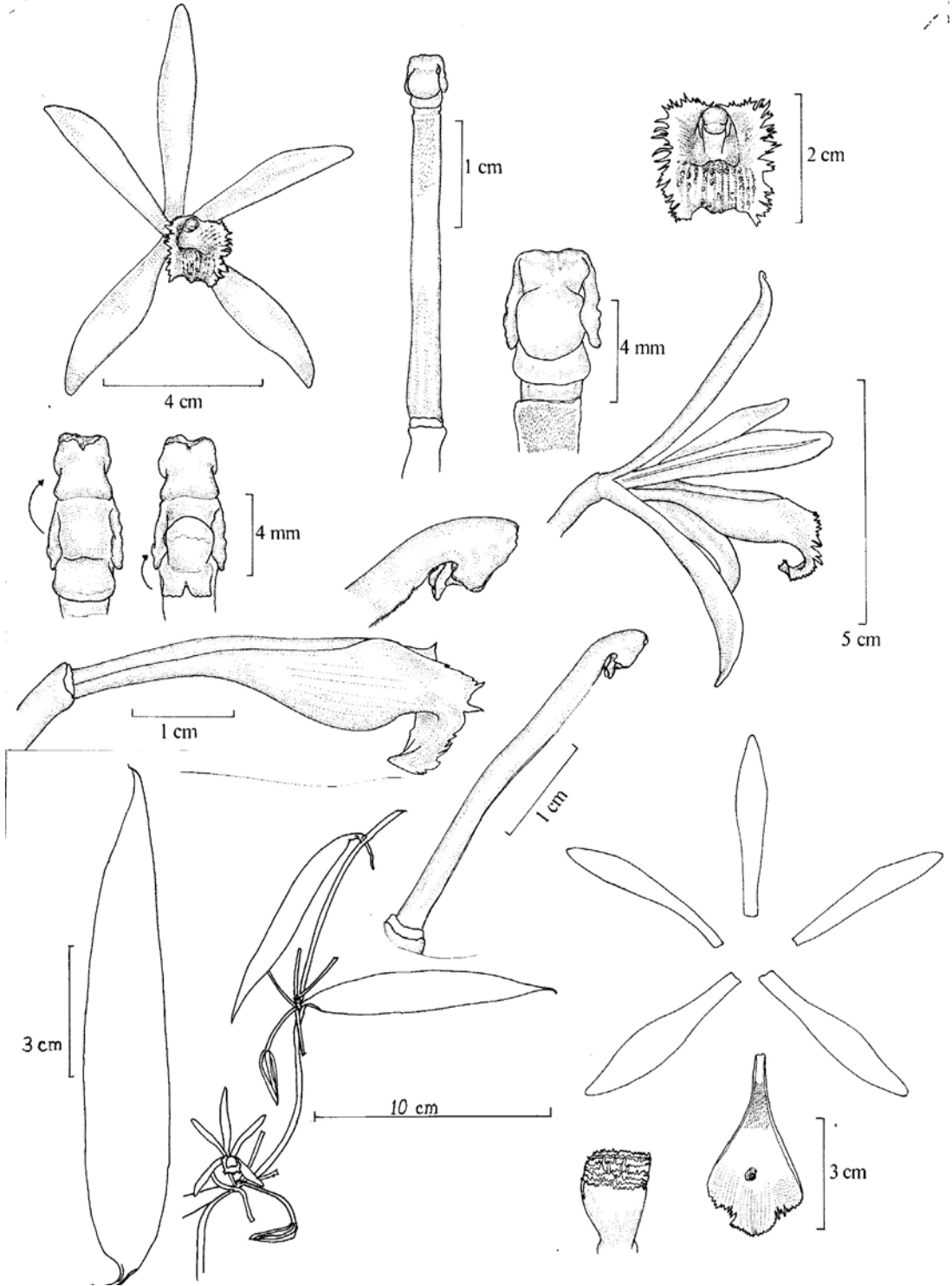


FIGURE 11. *Vanilla odorata* Presl. Based on *M. Soto 6617*. Drawing by R. Jiménez.

fragrance weak, green, fresh. **Ovary** terete, smooth, ca. 3 mm thick. **Dorsal sepal** linear to oblanceolate, apex acute, rounded, subcalyptrate, base attenuate-subunguiculate, concave, 9-veined, 47-54 × 8.0-8.3 mm. **Lateral sepals** narrowly elliptic to oblanceolate, oblique, apex subacute, rounded, subcalyptrate, base attenuate-subunguiculate, concave, ca. 12-veined, 44.5-52 × 9.5 mm. **Petals** obliquely linear to oblanceolate, somewhat arcuate, apex obtuse, rounded, sometimes emarginate, oblique, fleshy, slightly calyptrate, base long attenuate; concave; with a very conspicuous, axial, elevated, flat, keel at the abaxial surface, ending in a cylindric, free, adpressed process, ca. 1 mm long; ca. 11-veined, 46-53 × 7 mm. **Lip** attached to the column along the margins of the basal half (ca. 23-29 mm), tubular, cymbiform, the apex abruptly deflexed; axially grooved on the abaxial surface, the groove well-defined and deep; when spread out 42-49 × 19-26 mm; long unguiculate, the claw dense papillose at base and apex on the inner surface, the papillae digitiform, unicellular, 13-14 × 2.7-3 mm; the blade obovate-flabellate in outline, obscurely trilobed, ca. 20-veined, the veins branched in the distal third and slightly thickened; the lateral lobes narrow and obliquely obovate, margins long lacerate-fimbriate (cilia 1-3.5 mm long), ca. 25 × 8-9 mm; midlobe approximately subquadrate-semiorbicular, the margin undulate-crispate, lacinate, obscurely emarginate, 7-9 × 7-11 mm; **penicillate callus** at 29 mm from the base, 3-4.5 × 3 mm; made up by ca. 9 imbricate, flabellate-praemorse, retrorse, lacinate scales, sometimes united each to other along the lateral margins, with some adpressed processes on the surfaces; continuous towards the lip apex with 3 inconspicuous keels, progressively thickened, less defined, and more confluent at apex, almost forming an apical, fleshy cushion, ca. 14-15 × 2 mm, with 3-4 conic, prominent, retrorse papillae and many small, elongate warts; other warts on the veins of the lateral lobes. **Column** very elongate and slender, semicylindric, 33-38.3 mm long, 2 mm wide; ventral surface flat and papillose, the papillae digitiform, septate, bigger towards the apex, absent at the basal third; apex dilated, with vertical wings, inconspicuously trilobed, ca. 2 mm long, 3 mm wide; clinandrium prominent, transversely oblong, concave, ca. 2 × 3 mm. **Stigma** trilobed, the lobes emergent; rostellum a flabelliform, somewhat convex blade, ca. 2 × 3 mm, covering and parallel to the lateral lobes, quadrate, slightly divergent

each to other, ca. 1 × 1 mm. **Anther** versatile, attached to the clinandrium margin by a laminar, broad filament; body urceolate in outline, with 2 upper, ovoid, small, divergent lobes; 3 × 2.5 mm. **Fruit** narrowly cylindrical, slightly compressed, attenuate at apex, dark green, 17-17.5 cm long, 8-10 mm thick; strongly fragrant, aroma similar to that of *V. planifolia*. Fig. 11.

DISTRIBUTION: Mexico (Veracruz, Oaxaca, Tabasco, and Chiapas), Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and probably Brazil.

ECOLOGY: This species can be common in secondary vegetation derived from tall, evergreen, tropical forest and rainforest, in gaps or in slopes with cleared canopy in primary forests. It is known from the sea level to 650 m altitude. Flowering time is mainly in April and May, but the vanilla growers in the Oaxacan Chinantla mention other sporadic flowerings in August and November. The flowers remain open until 2:30 P.M.

The narrow, lanceolate to ensiform, long acuminate leaves, thin stems, translucent whitish-green tepals, white-greenish lip with the throat striped with pale yellow and the lacinate margins of the lip are characteristic. *Vanilla insignis* is very similar, but it has thicker, sulcate, rugose-papillose stems, broader, xeromorphic leaves, and the retrorse appendages of the callus are much more numerous, bigger and orange-yellow.

Mesoamerican specimens of *V. odorata* are very similar to that illustrated by Blanche Ames (Ames, Sched. Orch. 9: 1-6. 1925) based on Ecuadorian material and supposedly close to the type; perhaps the segments are slightly broader and the wings of the column have better-defined sinuses, and the lacinae can be shorter in the Ecuadorian and Colombian (e.g. *Fonnegra et al. 1784*) material. With these bases, the small differences do not seem to warrant the recognition of separate taxa.

Some specimens of *Vanilla odorata* from Belize have been identified previously in herbaria as *V. hartii* Rolfe, and a picture of *V. odorata* was labeled as *V. hartii* in "Native Orchids of Belize" (McLeish *et al.*, 1995). Soto (1989) reported *V. odorata* from Mexico based on a specimen with buds from Quintana Roo (*Cabrera 4611 & Cabrera*), but that specimen actually belongs to *V. insignis*.

Humboldt cited a "vanilla de Usila". From his

description it seems that the involved species was *V. odorata*, which is well-known by the Chinantecan Indians of the region, and grown on a small scale at the present time.

At the beginning of the 19th century some vanillas were used as vermicide in Mexico and Cuba, and that is probably the origin of the Sessé and Mociño name. In the same way, the name “lombricera” was applied to some vanillas in Cuba (Boldó & Estévez, 1990).

Vanilla odorata produces aromatic fruits, similar to those of *V. planifolia*, with a strong, pleasant fragrance; they are very much appreciated in the regions where the species is wild. In Chiapas they are occasionally used to flavor rums; in this area the species is much more common than *V. planifolia*, and actually it is the only vanilla collected for its beans in the Selva Lacandona, as in many other areas of Tropical America. In northern Oaxaca the species is grown as a curiosity in the plantations, intermingled with *V. planifolia*; the growers mention different cultural requirements from those given to *V. planifolia*, since it needs stronger sunlight. Although the fragrance is appreciated, the beans are difficult to manage, since they are attacked by fungi and because they dehisce if treated the same way as the fruits of *V. planifolia*; open fruits of vanilla usually bring a lower price. *Vanilla odorata* is found in dry to damp sites, usually in areas with higher rainfall than those of *V. planifolia*, and seems to be tolerant to a wide range of light conditions. *Vanilla odorata* is undoubtedly a species to be considered in any breeding program with commercial vanillas (see comments under *Vanilla tahitensis*, in “Excluded species”).

OTHER RECORDS: **MEXICO: VERACRUZ:** [cf., sterile] “Vainilla”. Vine on “Jimba” shrubs and on trunks of trees. Leaves leathery, glabrous. Common in some areas in dense forest, absent in others, Fortuño, Coatzacoalcos River, alt. 30-60 m, February 1937, *L. Williams 8919* F(897099)! **OAXACA:** In sylvis umbrosis prope Lobani, Chinantla, Oajaca, *Liebmann 6142* W(11759)! Tuxtpec, Ejido Chiltepec, “vainilla”, domina *Lonchocarpus*, *M. Sousa 947* MEXU [sterile]! Dto. Tuxtpec, Usila, Arroyo Iguana, vainillal de Silvano Bautista, ca. 250 m s.n.m., 24 abril 1992, *M. Soto 6617* & *M. Hernández* *AMO(x3; illustration voucher)! Dto. Tuxtpec, Mpio. San José Independencia, Cerro Clarín, en el extremo SW de la Presa Temascal, ca. 120 m s.n.m., 29 abril 1994, *M. Soto 8829a* & *U. Sánchez* AMO! AMO(in spirit)! same data, abril 1994, *U. Sánchez s.n. y 6* AMO(in spirit)! Mpio. Valle Nacional, Arroyo de

Banco, vainillal del Sr. Lázaro Pérez Justo, 250 m s.n.m. con flores, muestreada para fragancia; menos atacada por plagas y patógenos que *V. planifolia*, 23-IV-1997, *M. Soto 8501* & *M. Hernández* *AMO(flowers, photos)! San Felipe Usila, en cafetal, “vainilla tlapeusco”, 23, abril 1995, *M. Hernández s.n.* AMO(flowers in spirit)! km 49.8 del camino Sochiapa-San Juan Lalana, 1.2 km antes de San Juan Lalana, 210 m s.n.m. Cafetal derivado de selva alta perennifolia, en el fondo de cañada rodeada de encinares calientes. Terrenos de Galino Téllez, 18-III-1997, *M. Soto 8115* & *A. Cibrián* AMO(fruit)! Dto. Tuxtpec, Mpio. San José Independencia, Cerro Clarín, en el extremo SW de la Presa Temascal, ca. 120 m s.n.m., 29 abril 1994, *M. Soto 7631* & *U. Sánchez* AMO! AMO(in spirit)! **CHIAPAS:** alrededores del sitio arqueológico de Bonampak, vegetación secundaria derivada de selva alta perennifolia, 350 m s.n.m., abril 1981, *M. Soto 1001* AMO! Mpio. Ocosingo, km 5 del camino del Crucero San Javier a Bonampak, vegetación secundaria derivada de selva alta perennifolia, sobre suelos rojos arcillosos, ca. 350 m s.n.m. 26 junio 1996 *M. Soto 7959* & *R. Solano* AMO(fruit)! Mpio. Ocosingo: Estación de Biología Chajul, en el borde del Río Lacatúm; camino a Arroyo Miranda, selva mediana subperennifolia inundable sobre terrenos planos con *Scheelea* y *Sabal*, ca. 180 m s.n.m., muy escasa, 21 junio 1996, *M. Soto 7950* y *R. Solano* AMO(sterile)! **BELIZE:** Trail through light jungle, near Camp 2. Alt. 2000 ft. Wiss (vine) with glossy green succulent leaves and stems. No flower or fruit seen. 20.8.1976. *C. Whiteford 1316* MO(2584013)! **GUATEMALA: IZABAL:** [cf., sterile] Twining vine; leaves deep green, succulent; fruit green, thick and succulent, twisted, exuding clear thick liquid when crushed; faint vanilla odor. Quebradas, 19-22 May 1919, *H. Pittier 8589A* NY! US(1013492); **ALTA VERAPAZ:** “Vainillita” Chirujija Oxec.; near the Finca Sepacuité, April 23, 1902, *O.F. Cook & R.F. Griggs 735* *US(408445)! **PETEN:** “Vainilla”. Fleshy vine, Tikal National Park, Tikal, in botanal north of hotel, January 20, 1961 *E. Contreras 1841* *LL(fruit)! La Libertad and vicinity, Aug.-Nov. 1933, *M. Aguilar H. 164* *AMES(40519; sterile)! **HONDURAS: COLON:** Capuchin site east, mangrove forest. 1.8 mi strip on the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 mi NE of Trujillo on old road to Castilla. Lat. 15°57'30”N; Long. 85°54'30”W. 2 Feb 1981, *J. Saunders 1008* *LL(sterile)! *SEL(038496, fruit)! Lancetilla, 150 ft., *Yuncker 4993* NY! **NICARAGUA: SEGOVIA:** E of Jalapa, elev. 1600 ft., May-June, *A.H. Heller 6106* SEL(013289; 003851, drawing, fragments)! “Segovia Prov.”, *A.H. Heller s.n.* F(1598348)! without data, *A.H. Heller s.n.* SEL(003851)! **ZELAYA:** [sterile]” Vainilla”, bejuco, sobre árboles, Guamil de segunda clase. Area de Ocotál, Río Grande, Guamil o breñas sobre áreas pantanosas, a lo largo del Río Grande, Alt. 0-15 m, Abril 23, 1949, *A. Molina 2312*

F(1364505)! Cerro Waylawas, ca. 13°39'N, 84°48-49'W, elev. ca. 100-268 m; sheer dog tooth limestone peak and plain on E side of peak. Pendant epiphyte, sterile. 16 March 1978. W.D. Stevens, B.A. Krukoff 7385 SEL(049332; cf., sterile)! **COSTA RICA**: ALAJUELA: Upala, San José, Alrededores de Laguna Las Camelias, 10°28'N, 85°08'W 100 m, bejuco trepador, 19 Nov 1987, *G. Herrera 1346* INB(sterile)! MO(3709189)! LIMON: Hamburg Finca, on the Río Reventazón below Cairo, altitude about 55 meters. Large epiphytic vine; leaves and fruit dark green. "Vanilla nevermanii", "Vainilla". Febr. 19, 1926, *P.C. Standley & J. Valerio No. 48917* *AMES(32665; fruits)! *US(1309433)! [cf.] Hamburg Finca, on the Río Reventazón, *F. Nevermann s.n.* *AMES(33060; poorly preserved flowers)! **PANAMA**: PANAMA: [cf.] Barro Colorado Island, 10 Jan. 1940, *F.W. Hunnewell 16433* *AMES(sterile, 87907)! **COLOMBIA**: ANTIQUÍA: Hierba trepadora, tépalos externos verde amarillosos, internos amarillosos. Carretera Mutatá-Pavarandó, entre Haciendas La Esperanza y Mocarí, 150 m s.n.m. Marzo 6 1987. *R. Fonnegra, F.J. Roldán, J. Betancourt, B. Echeverry, O. Escobar 1784* K! *MO(3592235)! **PERU**: LORETO: Leticia on the Amazon River, September 1929, *L. Williams 3161* *AMES(43483; sterile)! Herbaceous vine. Yurimaguas, lower Río Huallaga; alt. about 135 m; dense forest, August 23-September 7, 1929, *E.P. Killip & A.C. Smith 29065* *AMES(43484; old inflorescences)! **BOLIVIA**: IXIAMAS: Best kind here, fruit fragrant, vine, common, climbing over small trees in damp forest, 15-20 ft, 1000-1500 ft alt, Dec 13 1921, *O.E. White 1115* *AMES(28024; fruits)! **BENI**: Rurrenabaque. Rank growing species; swamp woods, common. Fls. said to be white, fruits make good vanilla. 900-1000 ft alt., Dec 3, 1921, *O.E. White 1821* *AMES(28026; old inflorescence)! REFERENCES: Ames, Sched. Orch. 9: 1-6, fig. 1. 1925; Schweinfurth, Orch. Peru, Fieldiana 30(1): 43. 1958; Hamer, Ic. Pl. Trop. pl. 1193. 1984; Soto Arenas, Orquídea (Méx.) 13(1-2): 295-300, figs. p. 296, 297. 1994.

11. *Vanilla phaeantha* Rchb.f., Flora 48: 274. 1865.

TYPE: Cuba, *C. Wright 3351* W; AMES(71001, iso.)! BM(another specimen is *V. cf. poiteai*)! G(7889/109)! K(iso.)!

Vanilla planifolia var. *macrantha* Grisebach, Vcat. Pl. Cub. 267. 1866.

COMMON NAMES: "Tapia" (Panama).

Hemiepiphytic vine, branching, leafy. **Stems** terete, smooth, green, 4-12 mm thick (in dried condition); internodes 8-15.5 cm long. Aerial, free **roots**, terete, pale brownish, up to 10 cm long, ca. 2 mm thick; attaching roots strongly flattened up to ca.

5 mm wide. **Leaves** subsessile, the petiole twisted, canaliculate, up to 8 mm long; blade narrowly oblong to narrowly elliptic, base rounded-subcordate, apex acute-apiculate, chartaceous (xeromorphic), green, margins revolute, 10.3-19 x 2.2-5 cm. **Inflorescence** a 4-6-flowered raceme, 25-45 mm long, ca. 4-6 mm thick, peduncle 15-29 mm long, rachis, 11-15 mm. **Flowers** successive, 1 open at once, ephemeral, the segments spreading, at least 75 mm long; tepals greenish-white to cream, lip white stained with brownish at edges or orange-yellow. **Ovary** straight to arcuate, subterete, smooth, 42 mm long, ca. 4 mm thick. **Dorsal sepal** long oblanceolate acute-subacute, rounded at apex, subcalyptrate; base long unguiculate, attenuate, canaliculate, the claw ca. 24 mm long, ca. 3-4.5 mm wide, blade concave, ca. 10.5 mm wide, ca. 12 veined, smooth, thick and fleshy, total length, 62-74 mm. **Lateral sepals** strongly oblique, long oblanceolate, arcuate, apex acute, subcalyptrate and minutely warty on the apex of the outer surface; base long unguiculate, attenuate, canaliculate, claw ca. 22 x 5 mm; blade concave, 12-12.5 mm wide, ca. 14 veined, smooth, thick and fleshy, total length 58-72 mm. **Petals** long linear, arcuate, slightly sigmoid, apex subacute-obtuse, base long attenuate, canaliculate-conduplicate basally the rest concave, with an elevated axial, flat keel on the outer surface, ending in a triangular, acute, terminal process ca. 1 mm long, ca. 10-veined, thinner than the sepals, 61-73 x 8.5 mm. **Lip** attached to the column along the margins of the basal half (ca. 42-52 mm), tubular, trumpet shaped, conspicuously cymbiform, deepest near the middle, axially grooved on the lower surface, when spread out 62-72 mm; unguiculate, the claw canaliculate, with two rows of trichomes on the apical half, 26-34 x ca. 3 mm; the blade flabellate, somewhat trilobed, margin slightly undulate, ca. 36-veined, apex emarginate; obliquely long obovate, rounded 30-33 x 12-14 mm; midlobe distinct, transversely oblong, the margins conspicuously reflexed, revolute, emarginate, 5 x 11 mm; **penicillate callus** at 40-45 mm from the base, made up by ca. 12 congested, retrorse, approximately trapezoidal, fimbriate scales, the scales regularly united each to other along the lateral margins, ca. 9 x 5.5-6 mm, with an apical callus, low, inconspicuous, thickened. **Column** elongate, conspicuously sigmoid, 51-60 mm long; ventral surface lanuginose towards the

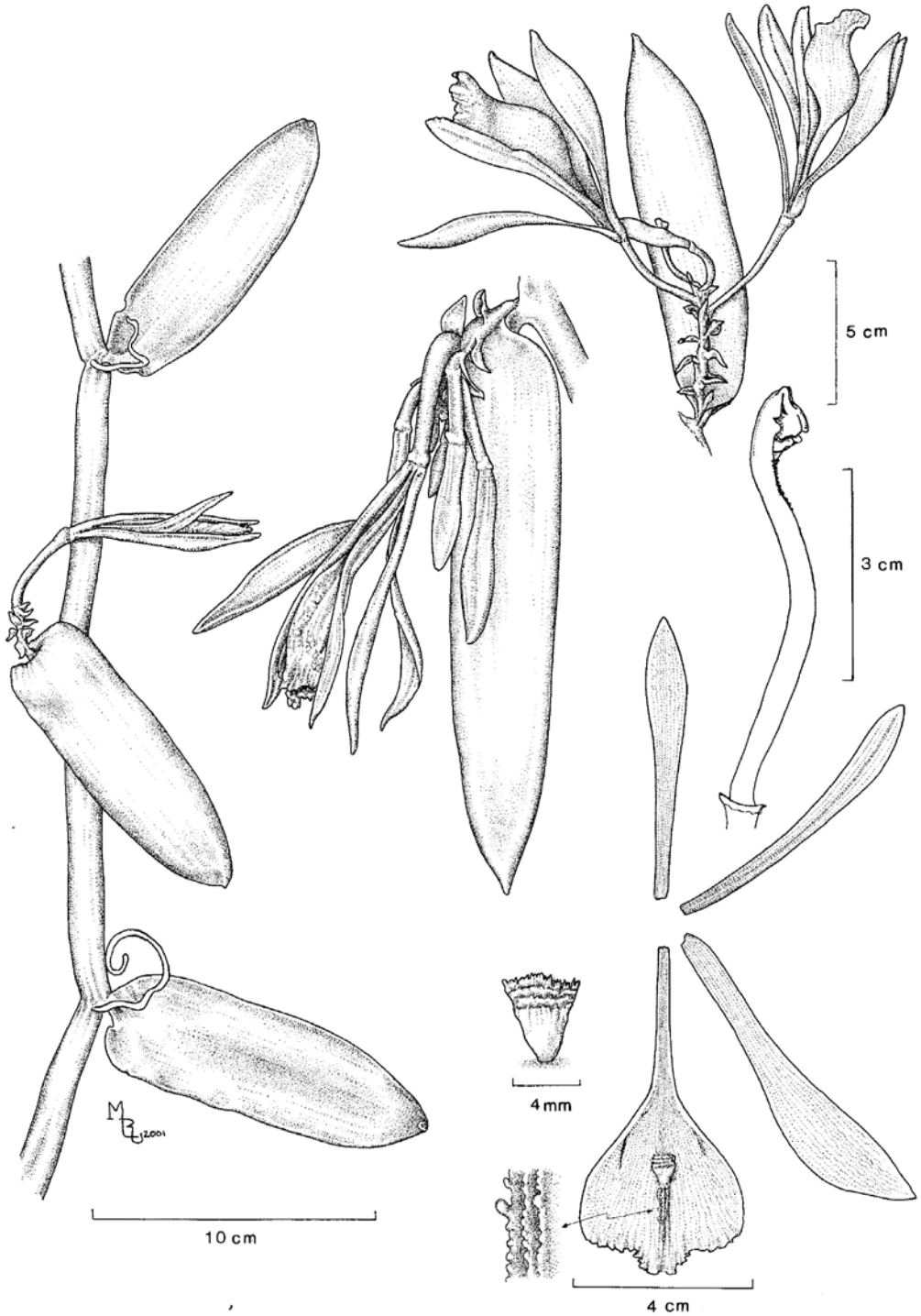


FIGURE 12. *Vanilla phaeantha* Rchb.f. Based on *R.S. Williams 588* (flower dissection), *O.F. Cook s.n. SEL!* (inflorescence with leaf) and *C.W. Powell 412* (inflorescence with 2 open flowers); *Dwyer et al. 4691* (column). Drawing by M. López.

apex, below the stigma; apex dilated, vertical wings somewhat bilobed, the lower lobe falcate, ca. 2 x 3.5. **Stigma** trilobed, with a convex, midlobe, ca. 3 x 4.5 mm, lateral lobes transversely oblong. Fig. 12, 16D.

DISTRIBUTION: U.S.A. (Florida), Cuba, Lesser Antilles, Venezuela, Trinidad, Mexico (Yucatán and Quintana Roo), ?Costa Rica, and Panama. It is unknown if similar plants found in Ecuador, Guyanas and Brazil belong here or to *V. bahiana*.

ECOLOGY: In Mexico this species grows in tropical deciduous or semideciduous forest near swampy areas, at about 100 m above sea level. Mexican specimens are juveniles and no flowering or fruiting specimens have been recorded. In Panama the species grows in coastal vegetation and in savannas with *Curatella*, *Clethra*, and *Roupala*.

A previous report of *V. phaeantha* from Central America was based on misidentified specimens of *V. calyculata*. *Vanilla phaeantha* is very common in the West Indies, but it has been scarcely recorded from the mainland, except from Florida. However, it reaches the coast of Venezuela (G. Carnevali, pers. com.), and also the Yucatan Peninsula and central Panama, in our study area. Mr. Neal Byrd, owner of Finca La Gavilana, Province of San José, Costa Rica, cultivates a *Vanilla phaeantha* that was apparently collected from the wild somewhere in Costa Rica. The only flowering specimens of this species that have been available to us are from Panama, where it seems to be common on the Pacific slope.

The oblong-elliptic, xerophytic, usually green-yellowish leaves are usually shorter than the internodes. The flowers are very large, with greenish tepals, and the lip is white with yellow stripes. It is related to *V. bahiana* Hoehne from Brazil. From the *V. planifolia* and *V. odorata* complexes it can be distinguished by its smooth disc.

OTHER RECORDS: **MEXICO:** **YUCATAN:** Cenote Mucul, Cerca de Sotuta, selva baja caducifolia, ca. 100 m s.n.m., *G. Carnevali* 4885 (cultivated specimen, not preserved, ITS sequence)! **QUINTANA ROO:** Mpio. Othón P. Blanco, Ejido Caobas, alrededores de la Sabana del Jaguactal, unos 21 km al sur de la carretera principal Xpujil-Chetumal, *A. Cibrián* 21, 23, *R. Jiménez*, *G. Carnevali* AMO(sterile)! **COSTA RICA:** **LIMON:** Guapiles, Los Diamantes, collected 26-12-2000, cultivated at Finca La Gavilana, Río

Savagres basin, *N. Byrd II-A-1-5 PANAMA: PANAMA:* Vine climbing up trees in low thicket. Farfan Beach; roadside thicket adjacent to beach. 30 March 1969, *J.D. Dwyer*, *L.N. Durkee* & *J.R. Castillón* 4691 *MO(1980689)! Balboa, “Tapia”, alt sea level, grows out in much sunlight, sepals & petals pale green; lip white with stain of brownish color at edge, flowers in April, 1924, *C.W. Powell* 412 *AMES(28219)! Ancon Hill, June 4, 1923, *W.R. Maxon* 6779 *AMES(33689)! *US(1180005)! Bismark above Panama, Fls. nearly white except greenish apex; climbing on trees several yards, March 12, 1908, *R.S. Williams* 588 NY! *US(678159; det by Schlechter as *V. pittieri*)! Common, sea level, February 1924, epiphyte, *Hort. Powell* 137, *C.W. Powell* 3507 *AMES(28290)! Climbing vinelike on the Farfan Beach area, forward dune-high beach community, 18 June 1971, *R.L. Lazor* 5358 SCZ(2262; sterile)! Fort Clayton, Farfan Beach area, vine with fl cream, 29 May 1966, *E.L. Tyson* 4106 MO(1917579)! SCZ(2263)! [cf.] Moist thickets; herbaceous vine; leaves very fleshy. Along the old Las Cruces Trail, between Fort Clayton and Corozal, December 3, *P.C. Standley* 29103 AMES(31440, sterile)! [cf.] Brushy slope; large herbaceous vine, common, Tumba Muerto Road, near Panamá, January 6, 1924 *P.C. Standley* 29731 AMES(31439, sterile)! **VERAGUAS:** Carretera Panamericana, 4.3 km al W de El Higo, ca. 20 km al W de La Mesa, sabana de *Curatella*, *Clethra* y *Roupala* con selva riparia de *Andira*, *Pithecellobium*, *Enterolobium* y *Acacia*, bejuco con frutos jóvenes, extendido sobre algunos arbolitos de la sabana, hojas muy pequeñas, tallos delgados, *M. Soto* 9920 PMA(ITS sequence)! **DOUBTFUL LOCALITY:** **CANAL ZONE** or **ALAJUELA**. Photo, April 15, 1925 O.F. Cook *SEL(011359; specimen; 111357 photo, the photo in envelope is of a membranaceous species)!

12. *Vanilla planifolia* G.Jacks., in Andrews, Bot. Repos. 8: t. 538. 1808.

LECTOTYPE: West Indies, without proper locality. Introduced into England by the Marquis of Blandford and flowered in the collection of the Rt. Hon. Charles Greville. The plate 538 was prepared from Greville’s specimen and was chosen as the lectotype (Garay & Sweet, 1974).

Lobus oblongus aromaticus Clusius, Exoticorum Libri Decem.: 72. 1605.

Araco aromaticus Hernández, Thes. Rev. Med. Nov. Hisp.: 38, fig. 1651.

Myrobroma fragrans Salisb., Parad. Lond. 2: t. 82. 1807, *nom. illeg.*

Based on the same specimen that served as the type of *V. planifolia* G. Jackson.

Vanilla fragrans (Salisb.) Ames, Sched. Orch. 7: 36. 1924; Stehlé, Fl. Descr. Antill. Fr. 1: 109. 1939; Portères, Enc. Biol. 46: 234. 1954.

Vanilla sativa Schiede, Linnaea 4: 573. 1829.

Holotype: "Baynilla mansa Hispano-Mexicanorum". Hab. sponte Papantlae, Misantlae, Nautlae et Colipae inque iisdem pagis colitur"; Schiede, May 29 [single leaf] BM!

Vanilla sylvestris Schiede, Schiede, Linnaea 4: 573. 1829.

Type: "Baynilla cimarrona, Hispano-Mexicanorum. Hab. Papantlae, Nautlae, Colipae", not located.

?*Vanilla carinata* Rolfe, J. Linn. Soc. London 32: 446. 1896. [or probably *V. gardneri* but the type is not useful]

Vanilla duckei Huber, Bol. Mus. Goeldi, Pará, 5(2): 327. 1908.

Type: *A. Ducke* GOELD.

Vanilla bampsiana Geerinck, Bull. Jard. Bot. Nat. Belg. 52: 345, fig. 1. 1982.

Type: Zaire, Bikoro: *Lebrun 1459* BR!

COMMON NAMES: "Vainilla mansa", "vainilla" (Veracruz), "Xanat", "shanat", "caxixánath" (Totonaco, Veracruz), "vainilla colibri" (Oaxaca), "tlilxóchitl" antique Nahuátl (Badianus manuscript), "Kuoley gm" (Chinanteco, Oaxaca), "zizbic" (Maya, Yucatán); "juju" (Tabasco).

Hemiepiphytic or rupicolous vine, much branched, leafy, up to 10 m high. **Stems** flexuous, terete, smooth, dark green, whitish dotted, sometimes the new stems covered with a whitish wax (Oaxacan plants), (6.5)11-12(13) mm thick; internodes 8-11 cm long. Terrestrial **roots** pubescent, 1.4-1.6 mm thick; aerial, free roots terete, 2.5-3.0 mm thick; attaching, aerial roots semiterete, flat on the surface in contact with the substrate, 3 mm wide. **Leaves** sessile, the blade, elliptic, oblong, narrowly oblong, usually with parallel margins, abruptly acuminate to subacuminate, somewhat oblique (variable), upper surface deep to pale green, paler on lower surface, 9.5-23 x 3.5-7.6 cm, ca. 1.3-2.4 mm thick in fresh. **Inflorescence** a 7-18(-70) flowered raceme, up to 26.5 cm long. **Flowers** successive, 1-2 open at once, segments variably spreading, most frequently the tepals ca. 40° with respect to the column;

ephemeral, showy, tepals pale green to whitish green, lip pale cream-yellow to yellow with ochre in the throat and papillae; ca. 62-64 mm high, 39 mm wide, fragrance weak, sometimes a cinnamon can be appreciated, herbal, or white (e.g. *Hymenocallis*-like). **Ovary** arcuate at base, upper part straight, terete, smooth, basally white, the rest green, with extrafloral nectaries, 57 mm long, 4 mm thick. **Dorsal sepal** narrow elliptic to oblanceolate, apex subacute, rounded, subcalyprate, base attenuate-subclawed, slightly concave, canaliculate basally, ca. 9-veined, 55-60 x 10-12 mm. **Lateral sepals** obliquely narrowly elliptic, to oblanceolate, apex subacute, subcalyprate, base attenuate-subclawed, almost flat, slightly canaliculate basally, margins slightly involute, ca. 10-veined, 54-60 x 12-13.5 mm. **Petals** obliquely long oblanceolate, somewhat arcuate, apex slightly reflexed, obtuse-rounded, oblique, notched, slightly thickened, base attenuate; concave, canaliculate at base; with a very conspicuous, axial elevated, flat keel at the abaxial surface, finishing in a cylindrical, free, ascending, free process, ca. 2 mm long; ca. 13-veined, 55-58.5 x 10-11 mm. **Lip** attached to the column along the margins of the basal half (ca. 31-35 mm), tubular, trumpet-shaped, very concave to cymbiform, slightly sigmoid, the apex abruptly flared, deflexed-recurved; opening subtriangular, 18 mm wide, axially grooved on the abaxial surface, the groove well-defined and deep; when spread out 49-55 x 24 mm; long unguiculate, the claw pubescent, trichomes short, yellow to ochre, 15 x 4 mm; the blade obovate-flabellate, trilobed in outline, ca. 36-veined, the veins branched in the distal third, and slightly thickened; the lateral lobes obliquely triangular-flabellate, margins widely undulate, denticulate towards the midlobe; teeth less than 0.6 mm long, ca. 27 x 10.5 mm; midlobe approximately subquadrate-transversely oblong, emarginate to deeply bilobed, the margin undulate-crenate, 5 x 9 mm; **penicillate callus** at 30-37 mm from the base, 5.8-6 x 4-4.5 mm; made up by ca. 8 imbricate, flabellate-praemorse, retrorse, lacerate scales, pale yellow, the distal ones bigger, sometimes united each to other along the lateral margins, continuous towards the lip apex with 2 conspicuous rows of papillae, and 2-4 inconspicuous rows, apical papillae bright green. **Column** very elongate and slender, trigonous-semicylindrical, 39-42 mm long, 2.5 mm wide; with vertical, flabellate to obscurely lobed-erose, acute to rounded, membranaceous wings, 2 mm

long, 4 mm wide. **Stigma** trilobed, the lobes emergent; midlobe a trapezoidal, convex blade; ca. 3 × 2 mm; covering and parallel to the lateral lobes, longitudinally oblong, slightly divergent each to other, ca. 1 × 1 mm. **Anther** versatile, attached to the clinandrium margin by a laminar, broad filament; body ovate-cordiform, 3 × 3 mm. **Fruit** straight to strongly arcuate, cylindrical-subclavate, thickened towards the apex, often 2-3 conspicuously sulcate in wild specimens; smooth in cultivated and many wild specimens; 10-30 cm long, 7-10 cm thick. Fig. 16E—F, 17D.

DISTRIBUTION: Imperfectly known. Mexico (Veracruz, Oaxaca, Chiapas, Tabasco, Quintana Roo, and probably escaped in Yucatán and southern Oaxaca), Guatemala, Belize, Honduras, and Costa Rica. It is unknown if the plants in other areas are native or escaped from cultivation. For example, in Panama it is known mostly from Barro Colorado Island and San Blas Province, perhaps an indication that it is escaped there.

The species seems to be escaped in Florida (cf. Luer, 1972), and in Jamaica (Fawcett & Rendle, 1910), two areas well botanized by experienced collectors. Foldats (1969) indicated that the species is common in Venezuela, but did not cite records; neither did Garay and Dunsterville include it in their works on Venezuelan orchids. South American wild specimens previously identified as *V. planifolia* and others from elsewhere outside Central America have proven to be misidentifications. On the other hand, there are some collections from Ecuador that match closely the Central American, cultivated material. It is doubtful that *V. planifolia* is native in regions outside of Mesoamerica. Supposedly wild specimens of *V. planifolia* from Rio Palenque Center, Ecuador, have proven to be *V. hartii*.

The original distribution in Mexico is also uncertain. Northernmost, wild-collected specimens come from the region of Córdoba, in Central Veracruz, some hundreds of kilometers southwards from the area where the species supposedly was domesticated in northern Veracruz and Puebla. Most collections come from northern Oaxaca, where great morphological variation has been observed; a single record from southern Oaxaca, on the Pacific slope, has not been confirmed by recent collections. The species is very rare in Chiapas. There are several old collections from

Yucatán, in the xerophytic thorn scrub of the northern part of the peninsula; we suspect that they represent escaped, old relicts from cultivated plants, since this habitat is very different from the moister forests where it is wild at present.

ECOLOGY: Dwelling in tall tropical evergreen or semievergreen forests, from 150 to 900 m, rarely to 1300 m altitude. The species seems to prefer moist forests, seasonally dry in spring, on calcareous terrain. It is absent in volcanic areas and in the wet tropical rainforests of Mexico. In moister areas it can be found in secondary, very young forests, or in large gaps. It flowers mainly in March to April, but varies from year to year, and flowering is rather gregarious in a region. Occasionally it flowers from February to May. Flowering seems to be a response to low winter temperatures, followed by strong sunny conditions in early spring.

Vanilla planifolia faces severe conservation problems in the wild. There are very few and scattered locations known at present; the largest populations in northern Oaxaca have been completely removed as a source of cuttings to establish new plantations; it is also almost extinct in Veracruz, where only two clones have been located in recent years. Only four isolated specimens have been located in Chiapas.

Vanilla planifolia is the vanilla of commerce, and the most widely planted species for its aromatic fruits.

The nomenclature of this species is very complex, since its history began before the Linnean system of nomenclature. The problem has been solved by Garay & Sweet (1974), who lectotypified the species with a plate based on the original plant (leaving aside the statement of the identity of an earlier Plumier's polynomial); it seems pertinent to reproduce here their observations: "Jackson regards Plumier's unpublished drawing of "Vanilla flore albo, fructa breviori, corallino" as representing his *V. planifolia*. A study of this plate, however, convinces us that it represents *Vanilla eggertii* Rolfe. Salisbury based his *Myrobroma fragrans* also in Greville's cultivated specimen, but cited in synonymy *Epidendrum rubrum* Lam. Since in his publication *Epidendrum rubrum* is an integral part of the protologue, he should have made a transfer of Lamarck's epithet. It is of further interest that Salisbury equates or rather confuses *Epidendrum rubrum* Lam. with Plumier's polynomial description

referable to *Vanilla eggersii* Rolfe.” Therefore, the widely used name *Vanilla fragrans* must be rejected, because it was based on an illegitimate name.

The plate selected as the lectotype is not accurate enough to permit the recognition of the species; especially the much fringed lip suggests another species of the group, such as *V. odorata* or *V. insignis*. Hooker (1891) also expressed concern about the identity of this plate, and recognized the differences among Andrews’ and Salisbury’s plates. However, the same Greville’s individual plant was illustrated and precisely described a year earlier by Salisbury, when he published his *Myrobroma fragrans*, the plate and description are much more accurate, and undoubtedly belong to the widely cultivated, “Mexican vanilla”, discarding the possibility of it being another related species. The history of *Vanilla planifolia* has been reviewed by Dillon (1942) and Bruman (1948).

The published plate (Flore d’Afrique Centrale, pl. 39) of the recently described *V. bampsiana* Geerinck, from Zaire, is indistinguishable from our concept of *V. planifolia*. There are no vanillas with lamellose transverse callus, fimbriate margins, long unguiculate lips and papillose apices outside of Tropical America.

VARIATION AND CULTIVARS: *Vanilla planifolia* has proven to be somewhat variable in flower size, degree of flower opening, lip color, lip concavity, development of the lip papillae, intensity of fragrance, development of grooves on the fruit, self-compatibility, etc. This variation initially led us to consider the existence of more than one species involved; especially because of the uniformity of plants in cultivation (the cv. “mansa”) compared with wild-collected specimens. However, it is possible that the narrow morphological variation seen in cultivated plants must be attributed to reduced genetic variation (Cibrian, Soto Arenas,). Studies of gas chromatography indicate that the floral fragrance of different forms is composed primarily of the same compounds (1-2-dimethyl-cyclopentane, ethyl acetate, 1-8-cineol and ocimene-trans); 1-8-cineol especially is well known to be a strong attractant for euglossine bees. Since *V. planifolia* is pollinated by *Euglossa viridissima* and maybe other species of the same genus, the fragrant, attractive compounds can be considered as evidence for the specific integrity of all the known forms.

The growers in Veracruz recognize different types in *V. planifolia*, and these perhaps represent different genetic individuals (clones), since no genetic manipulation or breeding programs have been conducted in Mexico. These clones are better treated as cultivars.

cv. “mansa” or “dura”

This is the form widely cultivated in northern Veracruz, and probably in Africa and Asia; the plants from Asia (except the Philippines) and Africa are descendant of the original type specimen grown by Greville and distributed to many botanic gardens during the 19th Century. It is unknown if more than one clone is involved, but the plants are very uniform in morphology. Different from many wild specimens are the non-sulcate fruits.

cvs. “acamaya”, “rayada”, and “variegata”.

The stems and leaves have yellowish stripes, alternating with the common deep green of the other cultivars (see Roulet, 1990). There are at least two different genetic individual with variegated plants (Schlüter *et al.* 2007). There seem to be no differences in molecular markers between one of this clones and ‘Mansa’, suggesting that it can be a sport (due to somatic mutation).

cv. “albo-marginata”

A cultivar with beautiful leaves, margined with white (see Roulet, 1990). It has never been found in Mexico, and it is probably also a sport of Madagascan origin.

cv. “oreja de burro”

? *Vanilla sylvestris* Schiede

The cv. “oreja de burro” is occasionally grown as a curiosity in the plantations of the region of Papantla. It is very similar to the cv. “mansa”, and difficult to distinguish except by experienced growers; the stems are slightly thinner, the leaves rather hanging, because the more elongate petiole, elliptic, abruptly acuminate, concave, with more prominent veins, and more greenish flowers. Once pollinated it forms a large fruit up to 30 cm long, usually bisulcate, but almost all the fruits are aborted in July, except sometimes when the pollen came from a different clone or from *V. pompona*; therefore, it is self-incompatible. Additional watering or feeding does not seem to maintain the fruits

on the plant. The occasional fruits are longitudinally sulcate; it is probable that this cultivar was the base for Schiede's *V. sylvestris*, since the sulcate fruits are cited in the protologue.

It is said that the cv. "oreja de burro" grows faster and with more vigor than other cultivars of *V. planifolia*; furthermore the growers say that it is not severely affected by fungal diseases. Some of the indicated differences between "mansa" and "oreja de burro" are statistically significant (Castillo and Engleman, 1993); however, the vegetative propagation of vanillas in the plantations has made many of them genetically uniform, and it is very probable that the observed differences are among clones and not between different taxa (species, subspecies or varieties) or indicative of a genetic substructure in *V. planifolia*. The "oreja de burro" has a floral fragrance similar to the cv. "mansa" and it is also visited by *Euglossa viridissima*.

Cuttings of "oreja de burro" are sold occasionally by unscrupulous growers to discourage the establishment of new plantations. We have observed hectares of plantations that were nonproductive due to large quantity of vines belonging to the cv. "oreja de burro".

Several wild collected plants are notoriously different from the specimens cited above, and it is very probable that they belong to locally differentiated populations. Among them, there are several specimens collected in Belize that look somewhat different, with small leaves, and flowers with a poorly-defined midlobe of lip. These specimens have also rather elongate rachis and the flowering time is from December to April. *Schipp S-971*, *M.A. Soto 8355*, *P.C. Standley 25064* are from Belize, Izabal, and Chiapas, from riparian habitats and they seem to be wild; however, leaf aspect is much more elliptic, and *M.A. Soto 8355* has more greenish flowers and much longer fruits. DNA sequences of *MAS 8355* is nested within the variation of *V. planifolia*, although with several autapomorphies, but we do not know if they represent only sequencing problems. Schlüter *et al.* have shown that *V. planifolia* has three rather different genetic groups, the cultivated group, the wild specimens from Mexico to Quintana Roo and the wild specimens from Costa Rica.

A specimen from Costa Rica [Esquinas forest. Area between the Río Esquinas and Palmar, sea level. May 2, 1950. Flowers pale green. *P.H. Allen 5532 SEL*

(011362)!] is somewhat strange, the leaves are clearly petiolate and elliptic, acuminate, but not abruptly and the inflorescence is very dense with bracts smaller than typical. The flowers are not well-preserved, but the lip does not seem lobed, and the warts on the apex of the lip are very obscure. Our impression is that its morphology is intermediate between *V. hartii* and *V. planifolia*, and therefore it may be a hybrid.

OTHER RECORDS: **MEXICO: VERACRUZ:** Rancho El Coscolín, El Escolín, Cerro Grande, Mpio. Papantla de Olarte, 350 m s.n.m., 20°29'N, 97°33'W, clima cálido seco, suelo arcilloso-arenoso, plantación de vainilla. Hierba trepadora de 2 m, flor y fruto, abundante. Flores con la base del perianto amarillenta. Fruto con la base adelgazada. Aborta 50-100% de los frutos. "vainilla oreja de burro", 25 Abr 1989, *R. Castillo M 211 & H. Cáliz de Dios AMO(x2)!* MEXU(678227)!

Other names applied in northern Veracruz, such as, "negra", "verde" or "amarilla" are apparently due to different exposure to light intensity.

OTHER RECORDS: **UNITED STATES: FLORIDA:** Dade Co. growing on trees in an extensive area in Cutler Hammock, on Biscayne Bay. Fls. greenish. May 15, 1976. *D.S. Correll & J. Popenoe 47216 NY!* Brickell Hammock, Miami, Dade County, *J.K. Small*, 19 Feb-March 22, 1915, NY! **MEXICO: SAN LUIS POTOSI:** Tanjasnec, Mpio. San Antonio, bosque tropical perennifolio, dooryard, vine, "vainilla", planted, 4 May 1979, *J.B. Alcorn 3006 *LL!* MEXU! **PUEBLA:** Bejuco, fruto verde, "vainilla", en cafetal, fecundada por jicotes, Yancuictlalpan, Cuetzalan, el fruto seco se usa como aromatizante y saborizante de atole y otros alimentos, *F. Basurto y R. Patrón 263 MEXU!* **VERACRUZ:** Rancho El Coscolín, El Escolín, Cerro Grande, Mpio. Papantla de Olarte, 350 m s.n.m., 20°29'N, 97°33'W, clima cálido seco, suelo arcilloso-arenoso, plantación de vainilla, hierba trepadora de 2 m, flor verde amarillenta, abundante, "vainilla mansa o fina", fruto alimenticio y para condimento, 25 Abr 1989, *R. Castillo M. 210 & H. Cáliz de Dios AMO(x2)!* MEXU(678228)! [cultivated] Predio Escolín, 12 km al NE de Papantla, 370 m s.n.m., trepadora, abundante, fruto verde, selva alta, secundaria, vainillal, suelo rendzina de color negruzco, 22 Junio 1987, *A. García 3226 MEXU!* [cultivated] Papantla de Olarte, 20°27'N, 97°19'W, "vainilla"; usos, para hacer figuras de vainilla, *F. Rosas C.I.P. 709 *XAL!* [cf.] San Andrés Tuxtla, El Vigía, al E de Cerro Blanco, 28 May 1967, *M. Peña 108 *AMES(11744, sterile)!* Estación de Biología Tropical de Los Tuxtlas, ca. 200 m s.n.m., selva alta perennifolia, *G.A. Salazar 2247 AMO(drawing)!* AMO(exsiccata, en FAA)! Volcano San Martín, on trees in dense forest, 5 May 1936, 95°11', 18°35', 600 m, *J. González*

sub E. Oestlund 5790 *AMES(51851, sterile)! Mpio. Atoyac, a un lado de la vía del tren, cerca del puente, selva alta subcaducifolia de *Bernoullia flammea* y *Dendropanax arboreous*, terreno cárstico, sobre piedras y árboles, 2 mayo 1995, ca. 400 m altitud, *M. Soto 7745* *AMO! Vainillal del Sr. Rafael Cardeña, Díaz Mirón y Río Nautla, Papantla, Veracruz. 180 m s.n.m. Muestreada para fragancia floral. 31-III-1995. *M. Soto 7648* AMO! [cf., fruit] A 800 m al norte de la casa de Genaro, ejido Vista Hermosa, Mpio. Tezonapa, 18°40'N, 96°40'W, alt. 500 m, selva mediana subperennifolia, primaria, suelo oscuro, arcilloso, bejuco perenne, escasa, fruto verde, nom. vul. "vainilla", 4-8-1986, *R. Robles G. 977* *XAL! [cultivated] Papantla, suelo poroso bien drenado con abundante materia orgánica asociada a *Gliricidia sepium*, *Erythrina berteroa*, *Bursera simaruba*, bejuco, flor verde amarillenta, nom. vul. "vainilla", "caxixanath" (Totonaco), 17-02-1985, *P. Reyes, N. Carcamo & N. Garcilazo s.n.* *XAL! OAXACA: Vine 10 ft high in woods between Los Llanos de Ozumazin and Río Chiquito, District of Choapam. Lat. 17°35', Long. 95°55', Alt. 700 ft., 1, May, 1939, *R.E. Schultes and B.P. Reko 727* *AMES(9034)! Cultivada en los vainillales de Santiago Tlapeuzco, Mpio. Usila, ca. 500 m s.n.m., *R. Medinilla s.n.* AMO(en FAA)! Cerro Machete, Distr. Pochutla, 800 m, Feb. 1941. *B.P. Reko 6279* *AMES(60425)! orquídea epífita, flor verde con la base blanquecina, acahual derivado de selva alta perennifolia, 3 km al W de La Esperanza, Mpio. Ixtlán de Juárez, Sierra Norte, *R. López G. 2* AMO(16698)! same data *E. Morales 1* AMO(16697)! Usila, Mpio. Usila, cultivada en los vainillales de la familia Bautista, cerca de la pista de aterrizaje, 90 m s.n.m. 25 abril 1992, *M. Soto 6672 & M. Hernández* *AMO(x 2; also in spirit)! mismos datos, aparentemente un clon con olor a canela y labelo teñido de café, *M. Soto 6673 & M. Hernández* AMO! mismos datos *M. Soto 6674 & M. Hernández* AMO! Dto. Tuxtepec, Mpio. San José Independencia, Cerro Clarín, en el extremo SW de la Presa Temascal, ca. 120 m s.n.m., selva alta perennifolia, 1 mayo 1994. *M. Soto 7630, U. Guzmán & Carlos* *AMO! Instituto Tecnológico Agropecuario, San Bartolo Tuxtepec, plantación a cargo de Jesús Pérez Meza. Abril 1996. *M. Soto 8040* AMO! Ejido La Gran Lucha, Mpio. Valle Nacional. Vainillal particular de Nemesio Miguel Martínez. Plantación proveniente de un sólo clon que originalmente crecía en las afueras de la comunidad. Plantación de 1 ha, 2500 plantas, de 3 años de edad. Plantación a 200 m s.n.m., en acahual derivado de selva alta perennifolia en ladera kárstica. 17-III-1997. "Ligüey" (Chinanteco). *M. Soto 8117 & A. Cibrián* *AMO! La Cueva, cerca de Cerro Verde, km 25.3 del camino Jalapa de Díaz-Usila, Oaxaca, selva perennifolia de montaña, 780 m s.n.m., muy húmeda, ca. 18°57'N, 94°44'W. Plantación de vainilla de José Roldán (aparentemente hay tres clones en la plantación). 21-IV-1997. Tal vez el mismo clon que *Soto 8477*. Flor muy cóncava que huele a canela. *M. Soto 8483 & M. Hernández* AMO! Mun. Santa María Jacatepec, predio El Aguila, al O de San Agustín, entrando por la Reforma, 28 km SO de Tuxtepec, carr. a Matías Romero. 17°50'N, 96°06'W. Elev. 550 m. Selva alta perennifolia. 19 Ene 1988. *R. Torres 11027 & E. Martínez* AMO(sterile)! MEXU(x3; sterile)! TABASCO: cultivada en el Jardín Botánico de Puyacatengo, en Teapa, fotografía! (Alderete y Capello, 1988); [cf., sterile] Teapa, 0.34 km al E de la Universidad Agraria de Chapingo, 17°31'31"N, 92°55'33"W, selva alta perennifolia, 28 enero 2002, *J. Calónico 21157 et al.* MEXU! Poblado de Nacajuca, 20 m s.n.m, selva mediana perennifolia, primaria, suelo negro arcilloso con abundante materia orgánica, bejuco perenne, 3 m, escaso, nom. vul. "juju", uso comestible, 3-10-1978, *R. Ortega, W. Márquez y B. Guerrero 858* *XAL! CHIAPAS: 17 km NO de Ocozocuatla, carretera nueva a la presa de Mal Paso, selva alta perennifolia, ca. 900-1200 m, *J. Castillo 833* (specimen in cultivation)! Palenque, abril de 1992, Alt. 450 m, R.M. *Comisión Geográfica-Exploradora, Sección de Historia Natural No. 7725* *AMES(21309)! 6 km al E de Emilio Rabasa, 1 km al NE de La Reyna, Ocozocuatla, 16°55'N, 93°38'40", 720 m, alrededores de una casa, huerto familiar y cultivos de maíz, *S. Ochoa 3659* CHIP! [cf., fruit] Reserva Ecológica "El Ocote", Mpio. Ocozocuatla, Alt. 750 m, selva alta perennifolia, primaria, suelo calizo, perturbada, hierba perenne, abundante, fruto vaina, trepadora, 14-02-1986, *M. Palacios-Ríos 2823* *XAL! Alrededores de la Laguna Ocotilito, cerca de Monte Líbano, selva baja perennifolia, 950 m altitud, *M. Soto 2836, 2840* AMO(slides, in spirit)! Mpio. Ocosingo, Estación de Biología de Chajul, vereda que conecta la vereda a La Granja con la de la Sabana I, a unos 500 m del Río Lacantúm, selva perturbada con bejucos y *Bactris*, terrenos ondulados y arenosos pero ocasionalmente inundables, ca. 200 m s.n.m. 16°08' N, 90°53' O. 13-IV-1997. *M. Soto 8355* AMO(sterile)! Estación de Biología de Chajul, montículo I, ruinas El Zapote, ca. 1 km de la estación. 200 m s.n.m. 16°08' N, 90°53'. En acahual de selva alta perennifolia con caña brava, muy joven, muy escasa. 20 junio 1996. *M. Soto 7947* AMO(sterile)! Estación de Biología de Chajul, junto al Río Lacantun, acahual con caña brava, muy joven, montículo I, Ruinas El Zapote; aparentemente es el mismo clon que *Soto 7947*, sobre *Cecropia obtusifolia*, muy escasa, vegetativamente igual a *Soto 8355*, que es otro clon. Flor más verde que las plantas cultivadas, hojas más anchas no planas y fruto corto y trigono, muy largo. Probablemente silvestre. 15 de abril de 2000, *M. Soto 9728, S. Maldonado, L. López & P. Schluetter* *AMO(x3)! Selva del Ocote, km 44.7 de la carretera Ocozocuatla-Malpasso, cerca de la presa, manchón perturbado de selva alta perennifolia con *Poulsenia armata*, *Ficus glabrata*, *Reinhardtia gracilis* y *Zamia splendens*, muy húmeda, sobre areniscas, 275 m s.n.m., probablemente silvestre. 21 abril de 2000, *M. Soto 9922, S. Maldonado, P. Schluetter, L. López & M. Soto* *AMO! Nahá, Mpio. de

Ocosingo; 27 km al SE de Palenque por la carretera fronteriza hasta el Crucero Chancalá, después 55.6 km por el camino de terracería hacia Monte Líbano, 16°56'-17°01' y 91°33'-91°38'; 900 m de altitud; bosque tropical perennifolio: Planta trepadora de unos 4 m de alto con flores amarillas. 6 mayo 1999, *A. Durán Fernández 1166* MEXU! **YUCATAN:** [sterile] "Vainilla" Yuc., "Sisbic" Maya, Cenote de Mayana, Yucatán, 1866, *A. Schott 215* F(276993)! In virgin xerophytic forest, April 1916, forests of Xbac, *G.F. Gaumer & Sons 23352* AMES(*71360, 71369)! *F(446854)! MO(948146)! NY! In virgin xerophytic forests, Izamal, April 1917, *G.F. Gaumer & Sons 23909* *F(466398)! *US(1268044; sterile)! [cf., poorly preserved] "Sisbic", June 4, 1899, *G.F. Gaumer & sons* F! Virgin forest near Chemax, on tree trunks, 29 Sep 1935, 87°56', 20°39', alt. 30 m, *O. Nagel sub E. Oestlund 5050* *AMES(51846, fruit)! **QUINTANA ROO:** Isle of Cozumel, Cenote Cedral, on tree trunks in mixed forest of *Achras zapota*, 2 sep 1935, 86°59', 20°21', 5-10 m, alt., *O. Nagel sub E. Oestlund 5001* *AMES(51852, fruit)! Ejido Hermenegildo Galeana, predios de Artemio y Constantino López Pascual, 18°10'33.2"N, 89°15'08.4"W selva alta subperennifolia alternada. 10-V-2008. *M. Soto 11370*, *L. Ibarra & C. López* AMO! **WITHOUT LOCALITY:** "1815 de Mexico, *Epidendrum vanilla*" [Sessé and Mociño collection] *Pavón* G! "Mexico, *Mr. Cowan* G! **BELIZE:** Machaca, forest shade, altitude 50 ft., height 35 ft., flower cream, common, 16 May 1934, *A. Schipp &-844* *AMES(40477)! **TOLEDO:** [cf.] "Vanilla". Vine, creamish colored flowers, scented, in broken cohune ridge, Feeders Road, 14 Miles, San Antonio-Punta Gorda Road, April 20, 1949, *P.H. Gentle 6721* *F(1599303)! *LL(x2)! NY! "Vianilla" Vine, flower greenish-white, scented, in acahual, on hill slope beyond San Antonio, January 30, 1952, *P. Gentle 7557* MEXU(511464)! *LL(x2)! "Vainilla", Fls. pale green, in cohune ridge, Bolo Camp, upper reach of Golden Stream, April 12, 1944, *P.H. Gentle 4521* *LL! "Vianilla", vine, flowers white, scented; in cohune ridge, near Jacinto Hills. December 30, 1944, *P.H. Gentle 5106* *LL(x3)! Quite common along river bank here in wet swampy places, still its difficult to secure flowering material as the squirrels get them. Flowers greenish yellow. Temash River. 100 ft alt., 30 ft. _ in. diam., 13th Mar 1935, *W.A. Schipp S-971* *AMES(43554)! Maskal Pine Ridge road, high ridge, yellow flowers, 3 March 1934, [?C.L. Lundell &] *P.H. Gentle 1234* AMES(*41360, *41361)! **GUATEMALA:** **BAJA VERAPAZ:** Bis 6 m lang. Bl. dichfleischig. gellegrün. Blt. mattschwefelgelle, sehr himfalling. Früchte. Blüht sehr reich. Am Rio Polochic über Tucurú, 900 m, Selten! 30.4.1882. *F.C. Lehmann 1436* G! **ALTA VERAPAZ:** Flowers pale greenish; lip slightly finely fringed with slight crests down middle. Vicinity of Finca Yalpemech, near Alta Verapaz-Petén boundary line, alt. 100-120 m. March 24, 1942, *J.A. Steyermark 45286* *AMES(62981)! *F(1195546)! **PETEN:** "Vianilla", vine, flowers green; Dolores, in low

forest about 2 km. 100 m south of village, May 3, 1961; *E. Contreras 2239* *LL! **IZABAL:** Large herbaceous vine, wet thicket, frequent, vicinity of Puerto Barrios, at sea level, June 2-6, 1922, *P.C. Standley 25064* *AMES(22674, fruit)! **EL SALVADOR:** Finca Las Canoas, 700 m alt. terr., climbing trees, mostly oaks, April 11th, 1969, *H.C. Clason sub F. Hamer 268* MO(3092269)! same data, near Ahuachapan, April 9th, 1978 *H.C. Clason sub F. Hamer 776* *SEL(049262)! "Vainilla", San Salvador, in garden, Vanilla seems to be cultivated in Salvador only as a curiosity, 1922, *S. Calderón 518* *AMES(22663, sterile) *US (1151498; sterile)! **HONDURAS:** **MORAZAN:** [cultivated] "vainilla", racemes 15-20 greenish-yellowish flowers, fragrant, vine 8 m long or more on *Cupressus lusitanica* in my yard, campus of EAP El Zamorano, alt 800 m. March 28 1990, *A. Molina 34346* *MO(4248893)! **ATLANTIDA:** [cf.] "Vainilla". Wet forest. Large herbaceous vine climbing over trees. Fls. pale green throughout. Lancetilla Valley, near Tela, altitude 20 to 600 m, Dec. 6. 1927, Mar. 20, 1928, *P.C. Standley 55583* *AMES(36947, sterile)! F(581081)! Climbing on tree, Lancetilla Valley, 159 ft alt., 8/12/1934, *T.G. Yuncker 4993* *AMES(105299, sterile)! **COMAYAGUA:** [cf., fruit] "Vainilla", frutos muy aromáticos cuando secos. Planta trepadora sobre el matorral en el bosque de montaña, alt. 1300 m, Marzo 31, 1963, *A. Molina 11777A* F(1620024)! **NICARAGUA:** **ZELAYA:** Logging camp near Quebrada La Talolinga. Elev. ca. 170 m. ca. 11°51-52'N, 84°26-27'W. Tropical wet forest. Climbing vine fruit green, *J.S. Miller & J.C. Sandino 1138* MO! **COSTA RICA:** **LIMON:** "Vainilla". Large epiphytic vine; leaves thick; fruit green; Hamburg Finca, on Rio Reventazón below Cairo, altitude about 55 meters. Febr. 19, 1926, *P.C. Standley & J. Valerio 48904* *AMES(32697, fruit)! *US(1309657)! in regione Atlantica: „Hamburg", 9 km ab ore fluminis Reventazón, inter *Musas cultas*, epiph! fl. viridi-lutei, altitudo: 15 m, Die: 2.V.1930, *G. Cufodonti 735* *AMES(37507)! W(1770)! Forest between Punta Manzanillo and Punta Nona, E of Manzanillo de Talamanca. Elev. ca. 8-12 m. 9°38'N, 82°38'W. Vine appressed-climbing in lower part, the fertile branches pendent, festooning small tree in understory of open forest atop coral bluffs along coast just E of Punta Manzanillo; borne ca. 3-4 m above ground. Flowers whitish-green, without fragrance (11:30 AM). Fruits green. Leaves thick, subsucculent. Flowers and fruits, 2 May 1985, *M.H. Grayum & G. Schatz 5257* CR(119858)! Pococi Cantón. Refugio de Vida Silvestre Barra del Colorado, Cerro del Tortuguero, summit ridge. 10°35'N 83°32'W, ca. 100-119 m. Vining to ca. 3.5 m above ground on small tree in secondary forest. Leaves very thick and fleshy. Corolla light greenish, the labellum longitudinally pleated internally and more or less lacerate marginally. 22 January 1997, *M.H. Grayum, B. Hammel, J. Schipper & L. Merrill 11141* INB! Cantón de Talamanca, P.N. Cahuita. Faja costeña de Limón. Sendero a

Puerto Vargas, 09°44'20" N, 82°49'30" W, 2 m. Planta trepadora, creciendo a orilla de sendero. Frutos inmaduros verde -claro y maduros verde amarillento. Común. 9 December 1993, *E. Lépiz 87, L. Poveda & V.H. Ramírez* INB! **PUNTARENAS**: Cantón de Golfito. Valle de Coto Colorado. Ribera del Río Esquinas. Boca Río Esquinas. 08°44'00" N 83°20'00" W, 30 m. Bejuco flores blancas, frutos verde-amarillentos. 22 December 1993, *M. Segura 264 & F. Quesada* INB! **CARTAGO**: Pejivalle, Very common in forest on ridges, seen also by riverside. No open fls found, May 1924, *G.H. Lankester 847* AMES(28561)! **PANAMA**: **PANAMA**: [sterile] Gross Lathrops trail, Barro Colorado Island, June 26, 1931, *L.H. Bailey & E. Zoe Bailey 374* AMES(37507)! [sterile] Wet forest; large herbaceous vine; occasional, Barro Colorado Island in Gatún Lake, altitude 120 meters or less, Nov. 18-24, 1925, *P.C. Standley 40897* *US(1251676)! Barro Colorado Island, Lutz Trail 300, vine, much scandent, seldom branching, sterile, July 10, 1970, *T.B. Croat 11177* SCZ(2261)! [cf.] Wheeler Trail, Barro Colorado Island, Oct. 26 1931, *O. Shattuck 230* AMES(71355, juvenile, sterile)! [cf., sterile] Wooded swamp; large herbaceous vine. Between France Field, Canal Zone, and Catival, Province of Colón, January 9, 1924, *P.C. Standley 30160* US(1225400)! **SAN BLAS**: Flowers pale green, April 28, 1933, *G. Proctor Cooper 287* AMES(*40380, *71354)! *F(771391)! NY! *US(1557502)!

REFERENCES: Hooker, Bot. Mag. 117: t. 7167. 1891; Rolfe, Journ. Linn. Soc. Bot. 32: 463. 1896; Duss, Ann. Inst. Col. Marsaelle 3: 601. 1897; Cogniaux in Urb. Symb. Antill. 6: 322. 1909; Ames & Correll, Orchids of Guatemala, Fieldiana: Bot. 26(1): 57, fig. 16. 1952; Cabrera, T. 1999. *Orquídeas de Chiapas*: 39; Luer, Nat. Orch. Florida 72. 1972; Garay & Sweet, Fl. Less. Antill. p. 44, fig. 7. 1974; Hamer, Orq. El Salvador 2: 372-373. 1974; Hallé, Fl. Nov.-Caledonie 8: 407. 1977.

13. *Vanilla pompona* Schiede, Linnaea 4: 573. 1829.

TYPE: "Baynilla pompona Hispano-Mexicanorum"; Mexico, Papanla et Colipa, *Schiede 1043*, "Vanilla pompona nob. interim Vaynilla pompona Papanlensis in sylvis Papanla, Ja. 29" BM (lectotype; Garay Fl. Ecuador Orch.); isolectotype W (sterile)!

Vanilla pompona is a variable, widely distributed species. We consider it rather to be a species complex.

The specific name is based in a Mexican specimen collected in central Veracruz. Mexican populations are apparently isolated from the rest of the populations of

the species because there are no known populations in Chiapas, Guatemala, Belize, or El Salvador. The taxon reappears only in Central Honduras and Nicaragua. This geographical isolation is correlated and probably the reason that Mexican samples in the ITS tree form a clade with high bootstrap support. The Mexican plants also have slightly different morphology, since the flowers and leaves are smaller, and the midlobe of the lip deeply emarginate, but the general aspect of the vine and flowers is very similar to the plants from Central and South America.

Perhaps a more detailed analysis of the flower may reveal more differences, but there is a notable lack of well-preserved flowers in the *V. pompona* group.

The rest of the samples of *V. pompona* have a paraphyletic relationship with the Mexican samples, but are more or less clustered into two groups. One of the groups encompasses the samples from Honduras, Nicaragua, Costa Rica and Panama. Differently from the Mexican and the South American vines, these samples sometimes have flowering shoots with rather small leaves, that is, they keep the juvenile stem morphology. Even though they do not form a monophyletic group within the tree it seems better to consider them another group within the species.

All the South American samples have common synapomorphic DNA characters, like peculiar nucleotide bases in certain positions and common deletions or insertions, although they also form a paraphyletic group.

We have considered recognizing these three groups in the *V. pompona* complex as different species, but the topology of the ITS tree, with the Mexican samples forming a monophyletic, derived group, and the other two geographic groups being rather paraphyletic, and the lack of constant, morphological traits have led us to give them subspecific ranks. Therefore, subspecies *pompona*, *pittieri*, and *grandiflora* are here recognized.

13a. *Vanilla pompona* Schiede subspecies *pompona*

COMMON NAMES: "vainilla platanillo", "platanillo", "vainilla pompona", "plátano", "vainilla cimarrona", "bania" (oaxaca), "nuguyu" or "nejuyu" (Oaxaca, Zoque), "vainilla", "litsmoya" (southern Veracruz; ?Popoluca); "vainilla gruesa" (Guerrero and S Oaxaca).

Hemiepiphytic, massive vine, little branched, leafy, up to 16 m high. **Stems** terete, smooth, pale green dotted with whitish, 10-24 mm thick; internodes 11-14.5 cm long. Aerial, free **roots** thick; terrestrial roots pilose, 4 mm thick; attaching roots conspicuously flattened on the lower surface, whitish-greenish. **Leaves** subsessile; blade variously shaped, ovate, widely elliptic, oblong-falcate, base widely rounded to subcordate, apex acute to subapiculate, coriaceous, very fleshy, brittle, pale green, 22-29 x 8-13.7 cm, 3 mm thick. **Inflorescence** 7-20-flowered raceme, up to 200 mm long. **Bracts** widely ovate, obtuse, rounded, concave to cymbiform, apex somewhat conduplicate, ca. 8 x 10 mm. **Flowers** successive, 1-2 open at once, ephemeral, tubular or with spreading segments, 58-83 (69.67±9.96) mm long; 7.5-10 cm in diameter; pale yellow, lip orange yellow, very showy; fragrance very strong, spicy, mint-like. **Ovary** arcuate, oval-subtrigonal in cross section, dorsiventrally flattened, arcuate, somewhat twisted, very slightly grooved on one face, smooth, green, 37-45 (42.29±2.71) mm long, 5-7 (5.85±0.78) mm wide, 3-4 (3.29±0.36) mm thick. **Dorsal sepal** long oblanceolate to spatulate, apex obtuse, rounded, subcalyptrate and minutely warty on the apex of the outer surface; base long unguiculate, long attenuate, canaliculate, the claw ca. 17-30 mm long, 8 mm wide in the broadest part, blade concave to somewhat conduplicate, 11-16.5 (14.06±1.73) mm wide, ca. 14 veined, smooth, thick and fleshy, total length 52-75 (66.37±6.42) mm. **Lateral sepals** long oblanceolate, oblique, apex obtuse, rounded, subcalyptrate and minutely warty on the apex of the outer surface; base long unguiculate, long attenuate, strongly canaliculate, the claw ca. 28 mm long, 9 mm wide in the broadest part, blade concave, 13-16 (14.87±1.13) mm wide, ca. 13-veined, smooth, thick and fleshy, total length 56-75 (68.8±6.79) mm. **Petals** oblanceolate-oblong, arcuate, slightly sigmoid and oblique, the upper margin more straight, apex truncate-rounded, base attenuate, basally slightly canaliculate, blade flat to lightly concave, with an elevated, axial, flat keel on the lower surface, ending in a triangular, acute, flat process, 2 mm long; conspicuously canaliculate at the apex of the outer surface, ca. 12-veined, 59-75 (67.83±5.58) x 11-17 (14.25±2.15) mm. **Lip** attached to the column along the margins of the basal half 30-40 mm (35,40,30,37,39) tubular, trumped-shaped, cymbiform, deepest near the middle, axially grooved

on the lower surface; when spread out 60-80 (71±8.52) x 29-40 (35.8±4.26) mm; unguiculate, the claw canaliculate, with rows of trichomes, 22-30 (24.2±2.92) x ca. 5 mm at apex, 3 mm at base; the blade flabellate to very obscurely trilobed, margin undulate, ca. 40 veined, apex deeply emarginate-bilobed; lateral lobes long triangular-ovate, oblique, rounded, 30-39 (35.2±3.48) x 10-15 (12.6±2.06) mm; midlobe inconspicuous, the margins fairly reflexed, revolute, deeply bilobed, ca. 6-10 (8±2) mm x 13-22 (17±3.4) mm; **penicillate callus** at 32-46 mm from the lip base, made up by ca. 10-14 congested, retrorse, approximately trapezoidal, laciniated scales, the scales regularly united each to other along the lateral margins, ca. 5.5-7 x 5-5.5 mm, continuous with 3 thick keels that soon become fused in a cushion like, claviform, rounded, rugose callus ending at the very apex; 18-23 (20.6±1.85) x 3.5-4.5 mm. **Column** elongate, conspicuously sigmoid, 43-59 (53±5.54) mm long, 3.2 mm wide; ventral surface lanuginose on the apical half, below the stigma; apex dilated, 4.5-6.5 mm wide; vertical wings triangular-flabellate, the lower margin acute, uncinata, ca. 2 x 4.5 mm. **Stigma** trilobed, the lobes emergent, with a convex rostellum, ca. 3 x 4.5; lateral lobes divergent each to other. **Fruit** variable, usually arcuate, trigonous, thick, green, blackish when rippen and strongly aromatic, 7.3-15 cm long, ca. 14 mm thick (n = 6). Fig. 13.

DISTRIBUTION: Mexico (Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, Veracruz). Specimens cited as *V. pompona* from Guatemala and Belize, and most from Honduras have turned out to be other taxa.

Vanilla pompona has a disjunct distribution. The type came from Veracruz, Mexico and this group of populations extends into N Oaxaca until the Tehuantepec Isthmus, but not reaching Chiapas. Subspecies *pompona* occurs in W Mexico (Nayarit to S Oaxaca), where characteristically small flowers whose segments do not spread widely are very common.

In the ITS tree all the samples of *V. pompona* from Mexico (both from the Atlantic and Pacific watershed) form a nested subclade with high bootstrap support (97%). Another clade within *V. pompona* includes material cultivated in Guadaloupe, and from Suriname and Guyanas, whose bootstrap value is moderate (70%). The rest of the samples of the complex have unresolved relationships at the base of the *V. pompona* clade, which has a 100% bootstrap value and is sister to *V.*

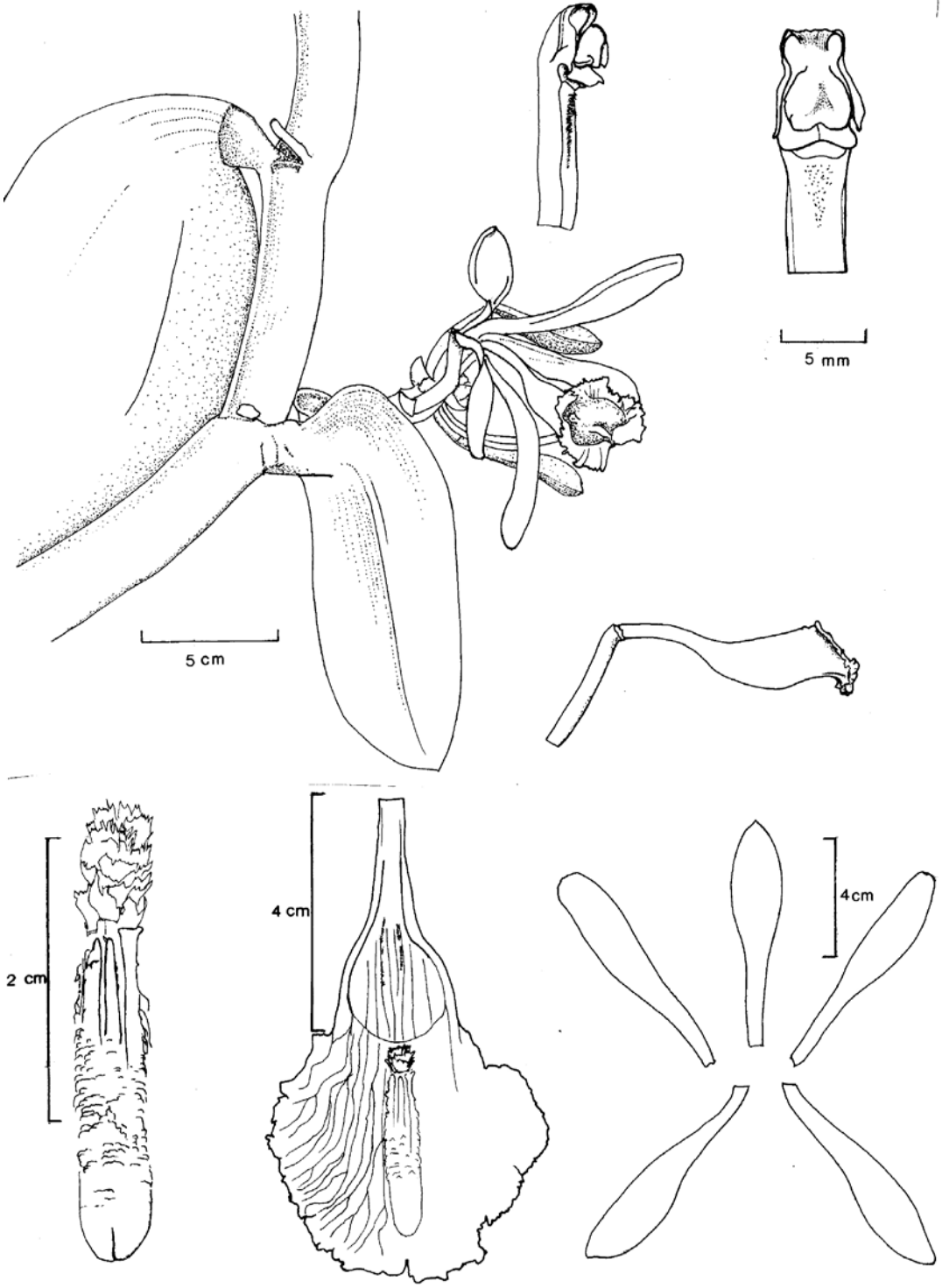


FIGURE 13. *Vanilla pompona* Schiede subsp. *pompona*. Based on *M. Soto* 7746. Drawing by *M. Soto*.

calyculata, a clearly different species.

The distribution, molecular, and morphological data suggest that subsp. *pompona* may be the result of a relatively recent colonization of Mexico through a rather long-dispersal event from Central American plants. We believe that we can recognize at least two taxa in the complex: *V. pompona* subsp. *pompona* and *V. pompona* subsp. *grandiflora* (Lindl.) Soto Arenas.

ECOLOGY: from sea level up to 1200 m, more common at 300-900 m; in several types of tropical forest (deciduous, subdeciduous, evergreen, lower mountain, gallery forests, in savannas or warm pine-oak forest, also in flooded areas) common in seasonally very dry areas; this species is usually absent from the wet forests, but occasionally can be located there in limestone outcrops. Flowering period from April to early June.

Vanilla pompona was described from sterile specimens collected by Schiede near Papantla and Colipa, in northern Veracruz, about 1829. The big plants, with very fleshy and thick stems bear huge, fleshy leaves, very variable in form, but always big in flowering shoots of Mexican plants. The large, deep yellow, and strongly fragrant flowers are very showy when they spread their segments (rarely in western Mexican populations); the short, thick fruit is strongly aromatic and very much appreciated by peasants, and also by vanilla connoisseurs. The odor of the cured fruits is typically heliotropin-like (Ehlers and Pfister, 1997). It is cultivated in small scale in the *V. planifolia* plantations, as a curiosity or charm, rarely offered to the commerce. On the Pacific slope, where it is known as “vanilla gruesa”, is very common in the coffee plantations, protected, but used only for local consumption.

Vanilla pompona subsp. *pompona* is somewhat variable; the specimens from the Pacific slope usually have bigger leaves and thicker stems, smaller flowers, and the perianth segments apparently never spreading; vegetative features probably represent a plastic response to drier conditions, and the flower size of some specimens of southern Oaxaca approach those of the Gulf watershed; the smallest-flowered specimens are found in Nayarit and Jalisco.

OTHER RECORDS: **MEXICO:** **NAYARIT:** Camino de Ruiz a Jesús María, ca. 200 m altitud, cafetal derivado de selva mediana subdecidua, abril 1986, *G. Salazar & M. Soto 2009, 2010, 2011, 2013, 2017* AMO! El Caimán, 100 m

sobre la brecha hacia El Naranjo, que sale del km 10 del camino El Cuarenteño - El Cora, encinares calientes mezclados con selva mediana subcaducifolia en las cañadas, *Quercus* cf. *conspersa*, *Byrsonima crassifolia*, *Bursera acuminata*, 490 m s.n.m., 21° 26' 22.2" y 105° 06' 09.6". Nos guió el Sr. Benito Decena Jiménez, de El Cora. 26/junio/1998. *M. Soto 8613* y *E. Huerta AMO! M. Soto 8617* y *E. Huerta AMO(x4)!* **JALISCO:** La Playa (oeste de Los Llanitos), Mpio de Puerto Vallarta, bosque subdeciduo, trepadora, 550 m alt., flores amarillas, muy escasa, *R. González Tamayo 884* *AMO! *LL! Mpio. Puerto Vallarta, entre Los Llanitos y Los Almacenes, *González Tamayo s.n.* dibujo! Mpio. Cabo Corrientes. above El Tuito, road to Mina de Cuale, *R. McVaugh 26397* **MICHOACAN:** Mpio. Aquila, San Pedro, Coalcomán, 550 m, 6-19-39, “Vanilla”, forest, vine, *G.B. Hinton 13815* *AMES(57796)! NY! *US(1805771)! Aquila, Tizupan, Coalcomán, 4-8-41, “Vanilla”, forest, *G.B. Hinton 15910* *AMES(60655)! NY! **GUERRERO:** Vallecitos, Montes de Oca, 9-13-1937, “vanilla”, on a tree, *G.B. Hinton et al. 11387* K! *US(2020421)! Sierra Madre, Guerrero- Michoacán, 400-1000 m alt., Mars 1900, Pl. grimpante & áttachant aux troncs d’arbres- Recólte des fruites d’Octobre à Novembre. Endroits ombragés, “Vainilla”, *E. Langlassé 941* *AMES(71358)! G(x2)! K! *US(386288)!. **OAXACA** (specimens from the Pacific slope): Pacific slopes of Sierra Madre, near Copalita and below Pluma Hidalgo, climbing on tree trunks, 26 Jul 1936, 500-1000 m, *O. Nagel & J. González sub E. Oestlund 6102* *AMES(51840)! km 190 Oaxaca-Pto. Angel. 14 mayo 1990. Flor prensada de material en líquido *O. Suárez 1153* AMO(15906; also in spirit)! Sanguijuela, Mpio. Juquila, 1200 m s.n.m., 21 sept. 1992, *V. Meza & M. Tovar s.n.* AMO(only fruit)! ca. San Gabriel Mixtepec, selva mediana subcaducifolia en cañadas con encinar seco en las lomas. ca. 600 m s.n.m. 17 de abril de 1992. *M. Soto 6607, N. Pérez y E. Martínez* AMO! Cerca de San Gabriel Mixtepec, cafetal en la zona de selva mediana subcaducifolia y encinar caliente, 800 m s.n.m. 11 mayo 1994. Fotografiada, flores semicerradas. *M. Soto 7632, A. Ryan, E. Sandoval A. Rojas & A. Martínez* *AMO! **OAXACA** (specimens from the Gulf slope): Consoquilla, /42, *Liebmann 288* W(11761, drawing)! 1859, *Cuming s.n.* G! Near Mogoñé, climbing on trees, Isthmus of Tehuantepec, fruit very fragrant, 95°01' 17°0', 100 m, 18 Feb 1935, *O. Nagel sub E. Oestlund 4574* *AMES(51841)! F(1257235)! *MO(1145434)! Isthmus of Tehuantepec. Near Mogoñé, climbing on trees, 95°01' 17°0', 100 m, 20 Apr 1935, *H. Knappe sub Oestlund 4781* *AMES(51842)! F(1257236)! *MO(1145435)! *SEL(011366)! *US(1809788)! San Juan Guichicovi, “vainilla”, hierba, pachine seco, en la orilla del camino, uso, con la fruta machacada, VIII-1986, *Nereyda Antonio & M. Heinrich UI 188* MEXU(431242)! ! Mpio. Sta. María Chimalapa: Arroyo Huahuagtzá, ca. 5.5 km al E

de Sta. María; lat. 16°55' N, Long. 94°39' O, alt. 250 m; acahual en área plana en orilla de arroyo (anteriormente selva); suelo negro. Bejuco; fruto verde, carne amarilla-verdosa con semillas negras; común; n.v. "bainia", "nuguyu" (en zoque); se usa en forma de aceite para el cabello para que de más olor, 5 septiembre 1984, *H. Hernández G. 396* *AMO(8094, fruit)! CHAPA! Mpio. Sta. Ma. Chimalapa: Arroyo Rancho Viejo, ca. 2-4 km al E de Sta. María; lat 16°54'N, long. 94°39'30"O; alt. 230 m; cañada con selva (rodeada por encinar) con *Poulsenia*, *Ficus*, *Brosimum* etc., suelos color café cascajoso. Epífita; fl. amarilla; "vainillo" (en castellano), "nejuyu" (zoque); frecuente; se usa para darle fragancia al cabello (se seca primero), 6 abril 1987, *H. Hernández 2418*, AMO(16964)! 4 km al W de la frontera Oaxaca-Chiapas, carretera a Tapanatepec, Dto. Juchitán, epífita, flor amarilla, poco frecuente, veg. riparia, suelo rocoso, 27 Marzo 1984 [botones], *R. Torres 4807* & *C. Martínez* MEXU! NY! Mpio. Santa María Guienagati, Loc. Dto. Tehuantepec. 3 km al N de Santa María Guienagati, carretera a Guevea de Humboldt. 16°43'N, 95°22'W; elev. 460 m, riparia con cafetal. Epífita, fruto verde, poco frecuente, 27 junio 1991, *A. Campos 3721* MEXU(578082)! ca. Valle Nacional, 1996, *J. Pérez Mesa s.n.* AMO(in spirit)! Terrenos comunales de San Agustín, Mpio. Sta. Ma. Jacatepec; a unos 2 km al W de San Agustín, selva húmeda con *Manilkara*, *Brosimum*, *Pseudolmedia*, con cafetal, a 350 m s.n.m. Planta silvestre de ca. 18 m de alto, protegida, con flores. 22-IV-1997. *M. Soto 8495*, *M. Hernández*, *F. Sánchez* y *M. Tensohua* AMO! VERACRUZ: Near Zacuapan. On trees, 12 feb 1932, 96°52' and 19°12' ca. 900 m, *O. Nagel sub E. Oestlund 2684* *AMES(41477, sterile)! From Mexico. Secured by Prof. P.H. Rolfs, in charge of the Subtropical Laboratory, Miami, Fla., while traveling in Mexico as agricultural explorer of the Office of S&PI in April, May, and June, 1905. This species is a very strong-growing vanilla. Produces the largest fruits and in considerably quantity. Secured near Papantla, Person interested: David Fairchild. *P.I. No. 14440* SEL(011358; photo)! Valle de Córdoba, 20 april 1865-6, *Bourgeau 2332* K! Region of Zacuapan, in brush wood, half shady, ca. 800 m, Jun 1935, *C.A. Purpus sub E. Oestlund 4852* *AMES(51839)! H. de la Higuera, 510 m s.n.m., vegetación riparia, bejuco perenne, abundancia regular, fruto aplanado [sic], septiembre 8, 1966, *M. Sousa 2721* *AMO(3443, fruit)! MEXU(277445, 296430, 277427; x3)! MO(4273614)! Cañada del Río Guazuntlán, 380 m s.n.m., selva alta perennifolia primaria, perenne, "litsmoya", colectada en fruto. Usos: seca se pone en vaselina y se unta en el pelo, septiembre 30, 1967, *M. Sousa 3276* *AMO(8592, fruit)! MEXU(fruit, 284554)! a 1 km al NE de Soteapan, 400 m s.n.m., encinar, epífita, escasa, perenne, 30 Sept. 1967 [estéril], *M. Sousa 3272* MEXU(284553)! "vainilla", La Ceiba, Municipio de Puente Nacional, bosque de árboles

varios en cañada, 100 m altitud, *F. Ventura 12355* *AMO(785, fruit)! MEXU(fruit, 235724)! Barranca de Monterrey, entre el manantial y la cueva del abono, Mpio. Axocuapan, alt. 380 m s.n.m., selva mediana subperennifolia, bejuco, fruto verde, nom. vul. "vainilla cimarrona", trepador, 02-01-1987, *M. Cházaro*, *L. Robles* & *J. Márquez 4376* *AMO(9026, fruit)! XAL(fruit)! El Remudadero, por la carretera Conejos-Totutla, Mpio. Paso de Ovejas, (19°17'N, 96°33' W), selva mediana subcaducifolia primaria, suelo arcilloso, pedregoso, en la barranca, bejuco perenne, 10 m, escasa, fruto verde, nom. vulgar "platanillo", fruto comestible, bejuco trepador, 01-11-1982, *G. Castillo C. 2747* *XAL(fruit)! Miraflores, 9 km al NW de Atoyac, Mpio. de Atoyac, 18°57'N, 96°49'W, alt. 900 m s.n.m., selva mediana subperennifolia, primaria, suelo cárstico, bejuco perenne, 8 m, flor amarilla, nom. vulgar "vainilla", 18-05-1985, *R. Acevedo* & *R. Acosta 195* *XAL! [cf., fruit] Límites de Veracruz con Tabasco, Mpio. Coatzacoalcos, 18°03'N, 96°06'W, selva baja inundable, primaria, suelo negro pantanoso, hierba trepadora, perenne, 6 m, fruto verde en vainas, nom. vulgar "vainilla", 18-05-1980, *J.I. Calzada 6096* F(1975502)! *XAL(fruit)! Alrededores de San Fernando, Mpio. Soteapan, 18°18'N, 94°53'W, alt. 720 m s.n.m., pinar-encinar, primaria, suelo rojo arcilloso, bejuco perenne, 1 m, escaso, fruto verde, 18-12-1978, *R. Ortega et al. 1021* F(1963648, flower)! *XAL(fruit)! 1 km al S de Palmillas, Mpio. Puente Nacional, 19°13'N, 96°46'W, 600 m s.n.m., selva baja caducifolia, primaria, suelo delgado, arcilloso, pedregoso, café, con poca materia orgánica, bejuco perenne, 4 m, fruto verde, 13-03-1985, *G. Castillo & M.E. Medina 4284* *XAL(fruit)! El Pochote, Mpio. Zentla, hierba, floración en mayo, *N. Deméneghi G. 558* *XAL(fruit)! Mecayapan, región de Los Tuxtlas; acahual derivado de encinar-pinar, 13/01/1998, *S. Cruz Ramirez sub M. Soto 8777* (cultivated plant)! Miraflores, cerca de Atoyac, ca. 750 m s.n.m. Acahual de selva mediana perennifolia submontana muy húmeda. Protegida o cultivada. Planta muy vigorosa, tallos 13-26 mm de diámetro, hojas hasta de 30 x 12.5 cm, flores de 9 cm de largo, no abiertas, sépalos y pétalos verdes exteriormente, parte interna amarillo-verde limón, labelo amarillo yema cocida con algunas líneas ocre, garganta profunda con la parte apical amarillo-naranja, aroma especioso, hierbabuena y algo más. 29-IV-1995. *M. Soto 7746* & *J. Arguijo* *AMO! El Angostillo, 34 km de Huatusco, ca. 14 km de Manuel González, Congregación El Pochote, La Reforma, Mpio. de Zentla, 500 m s.n.m.; selva baja caducifolia en barrancas basálticas; aroma fuerte a mentol, visitada por *Eulaema* en la casa de Julio Arguijo. 30-IV-1995. *M. Soto 7747*, *M.A. Flores*, *J. Arguijo*, *D. Deméneghi*, *M. Deméneghi* *AMO(x2)!

REFERENCES: McVaugh, Fl. Novo-Galiciana. 16: Orchidaceae: 351-353, fig. 115, 1985.

13b. *Vanilla pompona* Schiede subsp. *grandiflora*

(Lindl.) Soto Arenas, *comb. et stat. nov.*

BASIONYM: *Vanilla grandiflora* Lindl., *Gen. Sp. Orchid. Pl.* 435. (1840).

TYPE: Guyana Francesa, *Martin s.n.* (holotype, K-L!).

Illustr. Dunsterville y Garay *Venez. Orchid. Ill.* 1: 435 (1050, as *V. pompona*). N.v.: Palanda vainilla, Ecuador: vainillón.

Vanilla claviculata Duss non Sw.; *V. lutescens* Moq. ex Dupuis

COMMON NAMES: “vainillón” (French and British Antilles),

DISTRIBUTION: Apparently naturalized in the West Indies.

There is no adequate material from NW South America, but the specimens from the Amazon basin, Guyanas, Coastal Venezuela, and S Brazil are considered here to belong to *V. grandiflora*. It is unknown if the plants from W Ecuador are *V. pompona* or *V. grandifolia*.

ECOLOGY: Lubinsky, Van Dam & Van Dam (2006) report the pollination of *V. (pompona subsp.) grandiflora* by male *Eulaema meriana*, one of the largest of the euglossine bees. They also photographed a male *Eulaema cingulata* gathering scents from the mature fruit of this species. There has been at least one other report of euglossine bees brushing on *Vanilla* fruits (Madison, 1981). It is quite possible that the Euglossini may play a role in the dispersal of *Vanilla* seeds, as well as the pollination of the flowers.

Vanilla pompona is very similar to *V. grandiflora* Lindl. (“French Guiana: without precise locality, *Martin s.n.*, K-L!), and the latter is has been recognized as a synonym by most orchid taxonomists. However, *V. grandiflora* is different because it has a rather oblong lip blade, not flabelate to obscurely trilobed as in *V. pompona*. In *V. grandiflora* the flowers are larger, with the lip > 80 mm long, the callus 9-10 mm long and originated at ca. 60 cm from the base and the column is 60-75 mm long; also the apical thickening is less conspicuous in *V. grandiflora* and the flowers have usually spreading segments, while *V. pompona* is usually closed, although occasionally, specimens with spreading segments on sunny days are found, as the illustrated in fig. 13.

Vanilla lutescens Moq.-Tand. described from material of Paraguay [*M. Coudert*, cultivated at the Faculté de Médecine de Paris, the type, not seen; probable duplicate at W(35455)!] is also similar to *V. grandiflora* and maybe conspecific with it.

REFERENCES: Chiron, G.R. & R. Bellone. 2005. *Les orchidées de Guyane Française*: 138, photo p. 93.

13c. *Vanilla pompona* Schiede subspecies *pittieri* (Schltr.) Dressler, *comb. et stat nov.*

BASIONYM: *Vanilla pittieri* Schltr., *Fedde Rep.* 3: 106. 1906.

TYPE: Costa Rica: In der Wäldern an Ufern des Río Ceibo bei Buenos Aires, c. 200 m. M-H. *Pittier no. 6600*, blühend im Januar 1890, B(destroyed); AMES(24329; drawing of the holotype)! BR!

DISTRIBUTION: Honduras, Nicaragua, W Costa Rica and the Pacific side of Panama.

The available Costa Rican material is not very well-preserved, but seems to be more similar to the Mexican populations of the Pacific slope; the name *V. pittieri* Schltr. is available to these Costa Rican populations. The type of *V. pittieri* was lost in Berlin bombing; a sketch of the type made under R. Schlechter’s supervision, and a rather crude illustration of the flower is kept at AMES; the lip is shown as entire, with a very elliptic blade, as it had been prepared from an immature bud. There are additional specimens from the area of Buenos Aires, Puntarenas, that match our concept of *V. pompona*.

OTHER RECORDS: NICARAGUA: CHONTALES: ca. 2.8 km above (N of) Cuapa; ca. 12°17’N, 85°23’W, elev. 400-500 m; roadside, pastures, disturbed evergreen forest on hillside, and bank of small stream. One seen, climbing up trunk of large tree in disturbed forest near road, section of lower stem collected, *W.D. Stevens, B.A. Krukoff 3690* *SEL(049330; sterile)! SEGOVIA: *Oersted* W(19359)! Plant - Large thick (up to 2 cm) climbing leafy stems. Flowers- Large light yellow sepals and petals, yellow-orange lip. Light yellow column, orange on anterior face [mounted with description, notes an analytical drawing] *A.H. Heller s.n.* *SEL(003850)! NUEVA SEGOVIA: Quilali, ca. 13°34’N, 86°01’W, elev. 430 m, cultivated, said to have been collected wild in the vicinity about 10 years earlier; flowers yellow-green, fragrant, heavily visited by euglossine bees, fruits fleshy, dark brown, aromatic, 16 March 1980, *W.D. Stevens, B.A. Krukoff 16829*

*SEL(049331)! **ZELAYA**: Cerro Livico, 7 km northeast of Siuna, forest slope; elev. 500 m. Climbing trunk of tree 28 April 1978, D. Neill 3670 *SEL(047695; sterile)! **COSTA RICA**: **GUANACASTE**: Flores amarillas. Enredadera subiendo tronco de árbol, en chaparral o bosque poco denso dentro de sabana cerrada. A 5 millas al sur de La Cruz, Liberia. Alt. 200 m, febrero 11, 1963, *A. Jiménez M. 313* *F(1606969)! 550 m, *Calvo 1136* F(1456238)! Parque Nacional Guanacaste, Estación Maritza, sendero a la cima del Volcán Orosí. Bosque primario y secundario, 10°57.6'N, 85°29.6'W, 600 m. Planta epífita, creciendo sobre un árbol a 5 m de altura y a la orilla de una quebrada. Frutos verdes. 2 julio 1989, *INBio 132* INB! *CR(fruit)! **PUNTARENAS**: Cantón de Buenos Aires. Along the Río Ceibo, Ujarrás. 09°14'00" N, 83°18'00" W, 500 m. Thick stemmed vine; climbing high on trunk of tree in riparian forest. Lvs. succulent, deflexed. Just one young bud and one old, dry flower seen. 9 March 1993. *M. Grayum 10237* INB! Esparza Macacona, margen derecha, quebrada La Turbina. Bejuco trepador, botones florales verde tenue, flor de corola amarilla, aromática, 15 enero 1987, *G. Herrera & E. Herrera 466* MO(3594340)! **WITHOUT PRECISE LOCALITY**: "*Vanilla reichenbachii*", *Endres 270* W(16231, 16175, 16176)! Sepals and petals greenish yellow. Lip orange yellow. Pie del Turrubares, 150 m, March 6, 1926 *A. Alfaro 269* *AMES(31487, *31487)! In forest between Colonia & Las Huacas, May 25 1903, *O.F. Cook & C.B. Doyle 742* *US(474659)! "Costa Rica", dried leaf from *M. Godefroy-L.*, Paris, 1895 K! **PANAMA**: **PANAMA**: Low places contiguous to City, Alt Sea level. Grows in damp places. Climbs trees up to 40-60. Flowers yellow, with orange throat. Flowers Feb-March. 1919, *C.W. Powell 137* AMES(*23763; AMES 28290 is *V. phaeantha*)! Moist woods; large herbaceous vine, Río Paraíso, above East Paraíso, January 7, 1924, *P.C. Standley 29919* *AMES(31437, sterile)! *US(1225393)! Vine on west shore, Barro Colorado Island, March 11, 1931, *C.L. Wilson 119* *F(636191)! Barro Colorado Island, shores of Gatun Lake, South of Lab., Aug 28th 1929, *W.N. Bangham 458* *AMES(71357, fruit)! Near Canal Zone, *C.V. Piper s.n.* *AMES(36948)! Low thick scrub along R. Tecumen, north of Chepo road, up to 30 m. March 10, 1935, *A.A. Hunter and P.H. Allen 852* *AMES(42162)! *F(1329667)! *US(1976167)! Coastal thicket; large herbaceous vine; common, Punta Paitilla, January 12, 1924, *P.C. Standley 30788* *US(1229496)! Parque Nacional Altos de Campana. Epífita con botones florales verdes. Fuera del parque, a 1 km de la oficina del parque. Sendero de interpretación, 1 km al este del campamento de los guardabosques de INRENARE. Bosque húmedo tropical premontano. Elevación entre 800 y 900 m. 8°40'N; 79°55'W. 23 de abril de 1993, *M.D. Correa, E. Montenegro & E. Hidalgo 9460* PMA! Cerca de Cerro Azul, 14.8 km al N de la carretera Cd. de Panamá-Tocumen, camino Cerro Azul-Cerro Jefe, vegetación secundaria con *Terminalia* y *Byrsonima*, ca. 600 m s.n.m., trepadora, estéril,

toda la población con hojas elípticas, grandes y tallos gruesos, 4 junio 2001, *M. Soto 9921, G. Salazar, J. Linares y R. Gregg* PMA! in cult., at Smithsonian Tropical Research Institute in Balboa. Voucher: fragrance collection. 18 Mar 1979, *J.D. Ackerman 1354* SEL(039338)! In Powell's garden; large vine, Balboa, Non., 1923-Jan., 1924, *P.C. Standley 28570* *US(1225365; sterile)! **COCLE**: ca. 5 km al N de El Copé, entrada del Parque Nacional Omar Torrijos, vegetación secundaria abierta, derivada de bosque húmedo tropical premontano con *Vochysia*, ca. 700 m s.n.m. 2 junio 2001, *G. Salazar J. Linares, M. Soto y R. Gregg* PMA!

REFERENCES: Hamer, Orch. Nicaragua, Ic. Pl. Trop. pl. 1195. 1984.

14. *Vanilla sarapiquensis* Soto Arenas, sp. nov.

TYPE: **COSTA RICA**: HEREDIA: Sarapiquí. Llanura de San Carlos. Sardinal. Bosques residuales y tacotales camino a Finca Dos Loas. 10°31'45"N, 84°05'32", 70 m. Bejuco herbáceo. Sépalos verde crema, labelo blanco, columna con la punta negra, 10 May 1995, holo. *J.F. Morales 4082, E. Lépiz, V.H. Ramírez & A. Rojas* INB! iso. apparently at MO.

Vanillae costaricensis aemulens differt inflorescentiis bracteisque minoribus, floribus longioribus, labello suborbiculari, 3-lobato, callo duobus carinis incrassatis prominentibus in apicem confluentibus.

Hemiepiphytic vine, leafy. **Stems** 4 mm thick; internodes 6.5-7.8 cm long. Aerial **roots** flattened, ca. 2 mm wide. **Leaves** obscurely petiolate, the petiole canaliculate, ca. 7 mm long, 3.5 mm wide; blade elliptic, long acuminate, somewhat cuneate at base, membranaceous-chartaceous in dried condition, 15.9-19.5 x 4.8-7 cm. **Inflorescence** very different from the vegetative shoots, a 4-flowered raceme 5.5 cm long, internodes up to 1.5 cm long; peduncle ca. 26 mm, rachis ca. 2 mm thick. **Bracts** scale-like, ovate to lanceolate, acuminate, concave, 9 x 4 mm. **Flowers** successive, with rather spreading segments, showy, ca. 7 cm in diameter; tepals green-cream colored, lip white; of heavy substance. **Ovary** rather sigmoid, terete, somewhat thickened at base, smooth, inconspicuously sulcate, 42-53 mm long, 3-4 mm thick. **Dorsal sepal** rather spreading, convex, the margins reflexed, the apex slightly incurved, slightly undulate; elliptic, apex acute-subacute, extreme apex

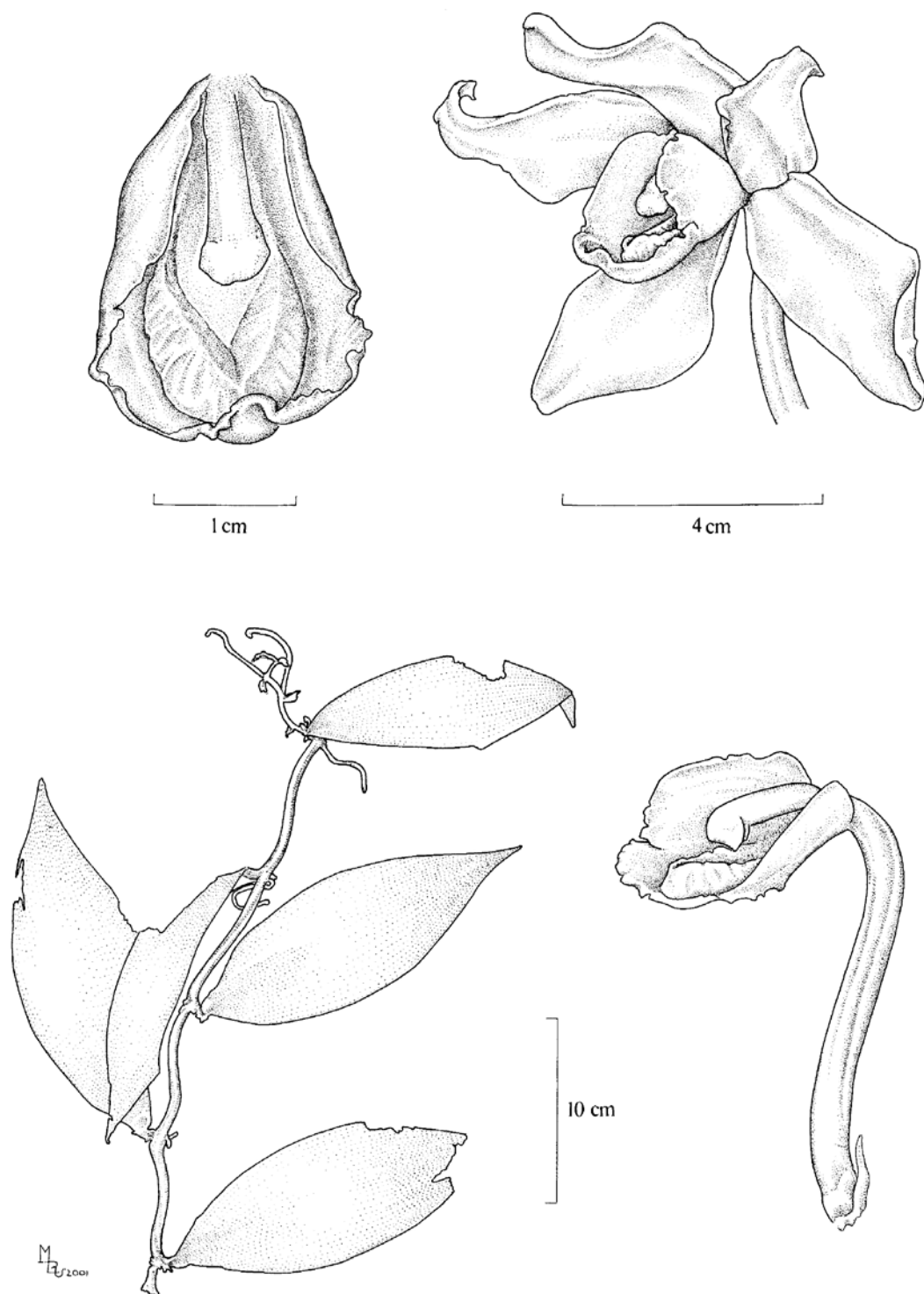


FIGURE 14. *Vanilla sarapiquensis* Soto Arenas, based on the type specimen, J.F. Morales 4082, Drawing by M. López.

conduplicate-subcalyptrate, rounded; base obtuse-rounded, ca. 10 veined, sparsely warty on the dorsal surface, 44 x 17 mm. **Lateral sepals** basally concave, convex at apex, the margins near the middle reflexed, the apex recurved, widely elliptic, obtuse, base obtuse-rounded, margins scarcely undulate, sparsely warty on the dorsal surface, 11-veined, 41 x 20 mm. **Petals** spreading, recurved at apex, slightly undulate on the upper margin, oblong-elliptic, oblique, subacute, base obtuse-rounded, 8-veined, smooth but axially sulcate on dorsal surface, 45 x 16 mm. **Lip** attached to the column 3 mm, ovate-suborbicular, obscurely trilobed in outline, constricted at 2/3; 32 x 28 mm, the base subcordate, slightly concave, with the lateral margins erect forming a throat around the column; midlobe concave, margins inflexed, incurved at apex, rounded, 8 x 16 mm; the lateral lobes semielliptic, the margins minutely pleated, 21 x 10 mm; **callus** arising above the middle, built up by a pair of broad, elevated apically confluent keels, the keels somewhat sulcate from the bottom to the crest, more elevated at distal part, widely triangular in cross-section on their distal part, 18 mm long, 5 mm wide. **Column** arcuate, semiterete, with a dilated apex, smooth, 21 x 4 mm. **Anther** protruding, semierect the distal part perpendicular to the column body; the anther separated from the surface of the lip. Fig. 14.

DISTRIBUTION: Known only from northern Costa Rica, in the Llanura de San Carlos; it is to be expected from adjacent Nicaragua.

ECOLOGY: Apparently in rainforest, at 70 m elevation. It was collected with flowers in May.

This species of the membranaceous group is known from a single collection from N Costa Rica. *Vanilla costaricensis*, is known from the same geographic area (Llanura de San Carlos), but *V. sarapiquensis* is distinct in its much shorter inflorescences with scale-like bracts (*V. costaricensis* has big bracts like those of *V. inodora*), larger flowers with much broader tepals, suborbicular, trilobed lip, and especially by the very different callus made up of two elevated, thick, sulcate keels, confluent in the apical part. In *V. costaricensis* the lip is subentire, ovate-flabellate, with the apex truncate or somewhat trilobed, but the lateral lobes at the apex are subequal or slightly longer than the mid lobe. In *V. costaricensis* the callus

is made up of a pair of flat, broad keels along the axial line, from the base to the beginning of the apical third, then separated in 3 low, erect, congested keels ending at the apex.

Vanilla mexicana has a distinctly trilobed lip, with the midlobe more protruding, 3-keeled, with the keels parallel. Also related is *V. martinezii* with much larger flowers, straight sepals, more rugose, basal keels, although the short inflorescence, with reduced bracts is similar.

15. *Vanilla trigonocarpa* Hoehne, Arq. Bot. Estado Sao Paulo, nov. ser. 1(6): 126, t. 139. 1944.

TYPE: BRAZIL:PARA: Matas de terra firme, Belém do Pará, flores em 23-11-1926 e frutos em 7-10-1926, *A. Ducke s.n.*. holo., HEPF(19445)!

Vanilla pauciflora Dressler, Orquideología 13(3): 229-232. pl. 1979.

TYPE: PANAMA: Prov. Panamá, carretera El Llano-Cartí, 10-15 km al norte de El Llano; 3 marzo 1976; sépalos verde pálido, pétalos crema verdoso, labelo blanco, lámina café-amarillo, fragante, *R.L. Dressler 5290*, holo. US(not seen).

Hemiepiphytic vine, leafy, up to at least 8 m high. **Stems** somewhat fleshy, 7-10 mm thick; internodes 4.8-7.5 cm long. Adventitious attaching roots dorsiventrally compressed, at least up to 6 cm long, ca. 4 mm wide; adventitious free roots subterete, ca. 3 cm long, 2 mm wide. **Leaves** petiolate, the petiole 1.5-2.5 cm long; blade elliptic or elliptic-oblong to obovate, long acuminate, leathery, relatively thin, 15-30 x 5.5-7 cm. **Inflorescence** usually on the lower part of the stem, a 1-2(-4) flowered raceme, 13-15 mm long. **Bracts** lanceolate, 15-20 mm long. **Flowers** with spreading segments, sepals pale green, petals greenish cream, lip cream, the blade yellow-brown with a white margin, the throat with yellow-brown veins. **Ovary** ca. 4 cm long. **Dorsal sepal** lanceolate, obtuse, subclawed, the claw ca. 40 mm long, 8 mm wide, 11-11.5 x 1.6-1.8 cm. **Lateral sepals** elliptic, subclawed, the claw ca. 40 mm long, 8 mm wide; 10.5-11 x 1.8-2 cm. **Petals** narrowly oblanceolate, obtuse, with a prominent rib on the outer surface, 10.8-11 x 1.6-1.8 cm. **Lip** attached to the column along the margins of the basal half (ca. 6.5-7 cm long), when flattened 11.5 x 5.5 cm; unguiculate,

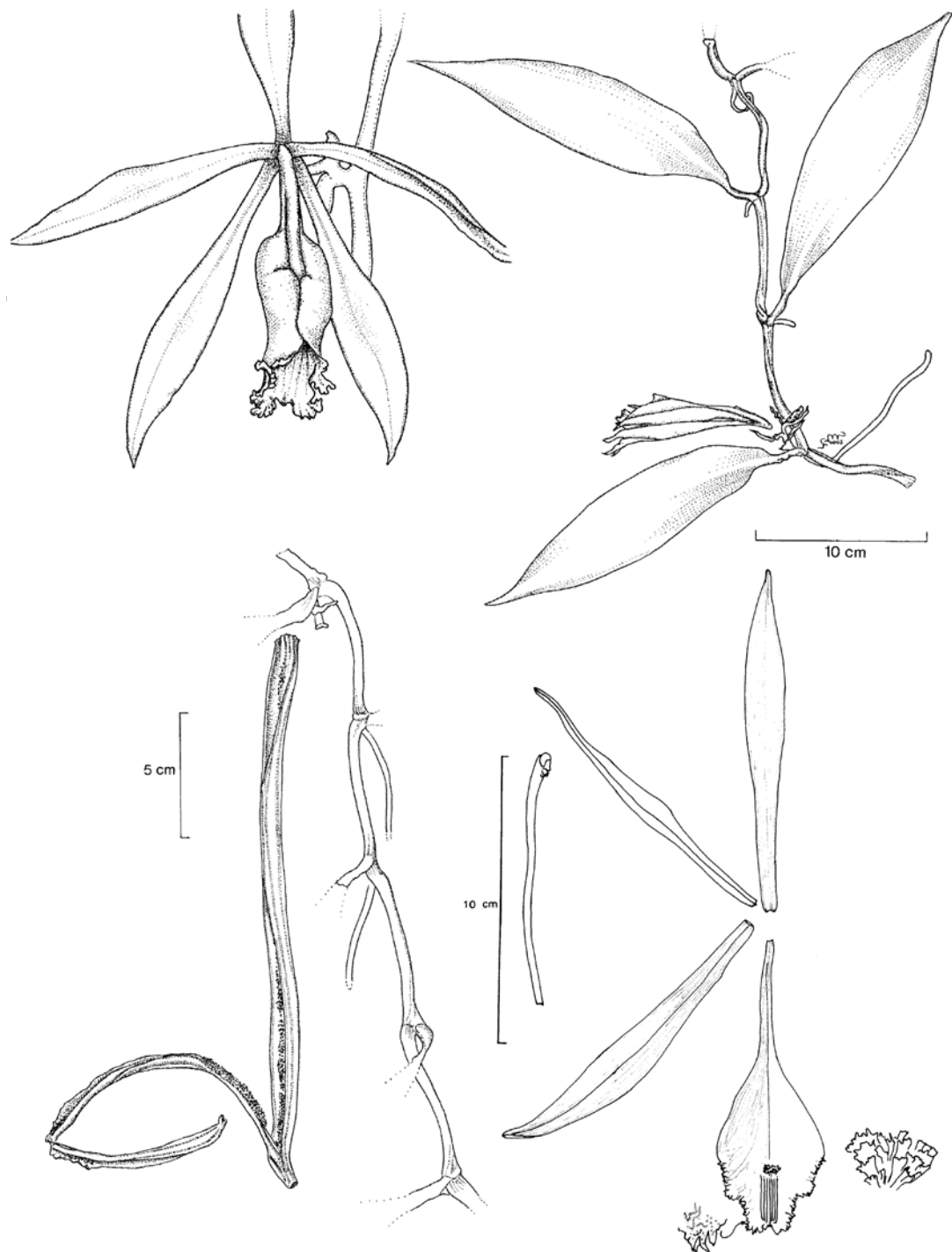


FIGURE 15. *Vanilla trigonocarpa* Hoehne. Based on *McPherson 11286* (plant, flower dissection), *Dressler 4750* (fruit), *Collingram & Ugoccioni 912* (flower, lateral view) and *Dressler s.n.* published picture. Drawing by M. López and M. Soto.

claw ca. 4 cm, then expanding abruptly and somewhat campanulate, inflated blade; the blade entire, margin strongly ruffled, ovate, ca. 11.5 cm long; **penicillate callus** made up by several lacinate scales, 5 x 5 mm; with a verruculose ridge running toward the apex; lip apex strongly veined. **Column** elongate, ca. 80 mm long, slightly arched, ventral surface pilose toward the apex (for ca. 3 cm); with small wings. **Stigma** trilobed, the lobes emergent, the mid-lobe the largest. **Anther** ventral, 6 x 4 mm. **Fruit** cylindrical, 20-23 cm long, ca. 1.8 cm wide; somewhat triangular in cross-section, dehiscent; the seeds subspheric, somewhat flattened, black and shiny, ca. 0.6 mm long. Fig. 15.

DISTRIBUTION: Costa Rica, Panama, and Brazil, and probably in the intermediate areas.

ECOLOGY: From very wet rainforest, from 120 to 350 m altitude; it can be common in certain areas. Flowers in Central America in January-February, and July; perhaps all year. Hoehne (1945) indicates that the flowers have a disagreeable fragrance, but that of the fruits is pleasant. Dressler (pers. com.) has observed males of *Euglossa asarophora* pollinating this species in Panama.

This species has been known in recent years in Central America as *Vanilla pauciflora* Dressler, but the Central American specimens are apparently conspecific with the Brazilian plant earlier described by Hoehne as *V. trigonocarpa*.

Vanilla trigonocarpa is somewhat variable in the form of the apical lobe of the lip, deeply retuse in the type and truncate to slightly emarginate in the Central American specimens. It is also variable in the development of the lacerate margins. The type specimen is minutely lacerate, as it is the specimen *T. Antonio 3645*, however, other specimens are deeply lacerate, as *G. McPherson 11286*.

Vanilla trigonocarpa is distinguished by the very large flowers on very short racemes with only 1-4 flowers with lanceolate, long acuminate bracts; the inflated lip, and strongly ruffled margins are also characteristic. It is probably related to *V. espondae* (and perhaps to *V. sprucei*), from Colombia, with flowers of the same color, but with shorter and broader segments, and the lip with an oblong-rounded midlobe covered with digitiform papillae, up to 3.5 mm long. Molecular analyses show that *V. trigonocarpa* is the most basal

species among the American penicillate Vanillas.

OTHER RECORDS: **COSTA RICA:** PUNTARENAS: at base of Osa Peninsula, ca. 25 km E of Rincón along newly improved road; elev 350 m, climbing on tree in mature rainforest, 4 Jan 1986, *P.M. Catling & V. Brownell C24.1* **AMES!** **PANAMA:** PANAMA: El Llano-Cartí road, 10.1 miles from highway, on trail to west; 9°15'N, 79°00'W; c. 350 m. Epiphytic on trunk; perianth green-white, the frilly portion of lip brown, 16 July 1987, *G. McPherson 11286* *MO(3499115)! about 10 km north of El Llano, 29 January 1974; vine, flowers borne from leafless stem, sepals and petals greenish cream, lip cream, streaked with brown-yellow within, center of limb brown-yellow, *R.L. Dressler 4571* (PMA, SEL); El Llano-Cartí highway, 10-12 km north of El Llano, 12 September 1974; climbing vine, about 8 m, *R.L. Dressler 4750* PMA, SEL *US(2952908)! **COCLE:** On the Atlantic side, ca. 5 hr walk from sawmill at El Copé. Along slopes above Norte Río Blanco near small village of Caño Sucio; elev. 400-500 ft. Epiphyte vine on side of tree; flowers a beautiful cream white; lip yellow - very fragrant, 2 Feb 1980, *T. Antonio 3645* *MO(2928700)! **WITHOUT LOCALITY:** leg.: Collector unknown. Selby Accession: 89-0281. Growing in Selby Display House. 26 April 1991. Coll. *Ingram & Ugocioni 912* *SEL(065176)!

REFERENCES: Hoehne, Fl. Bras. 13(2): 28, t. 20. 1945.

Excluded species

Vanilla barbellata Rehb.f., Flora 48: 274. 1865.

A horticultural specimen grown in Austria, supposedly from Cahuita, Costa Rica, seems to be the West Indian *V. barbellata*. There is a plate prepared by the artists of the Royal Botanical Expedition to New Spain, circa 1800 (Hunt Library; tracing at Library of MEXU (as “112 *Vanilla mexicana*”), G, and tracings probably elsewhere) that represents this species. The flower has scale-like leaves and hirsute lip. The Mexican origin of the plant is doubtful, since there are no confirmed records of leafless vanillas in mainland Mesoamerica. Many other paintings labeled as from Mexico (“de México”) are actually Cuban plants, prepared during the stay of the Expedition at the island. As far as we know, *Vanilla barbellata* has been found only in Bahamas, Florida, Cuba, Puerto Rico, and the Virgin Islands.

Vanilla mexicana Miller, Gard. Dict. ed. 8: n. 1. 1768.

TYPE: Haiti, *Plumier s.n.*, the holotype is Plumier's original drawing at P; reproduction Plumier, Nov.

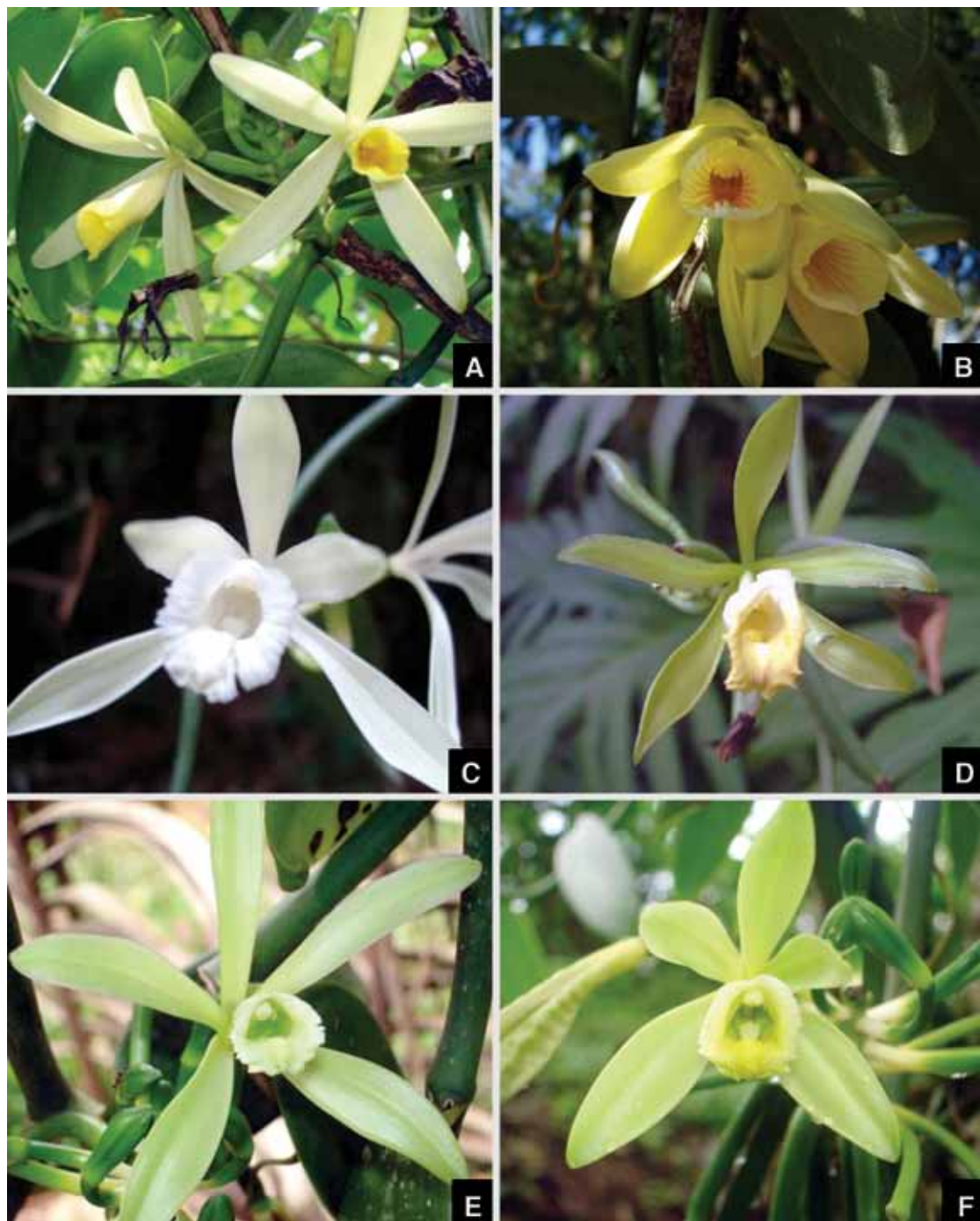


FIGURE 16. A — *Vanilla cribbiana*. B — *Vanilla dressleri*. C — *Vanilla hartii*. D — *Vanilla phaeantha*. E, F — *Vanilla planifolia*.

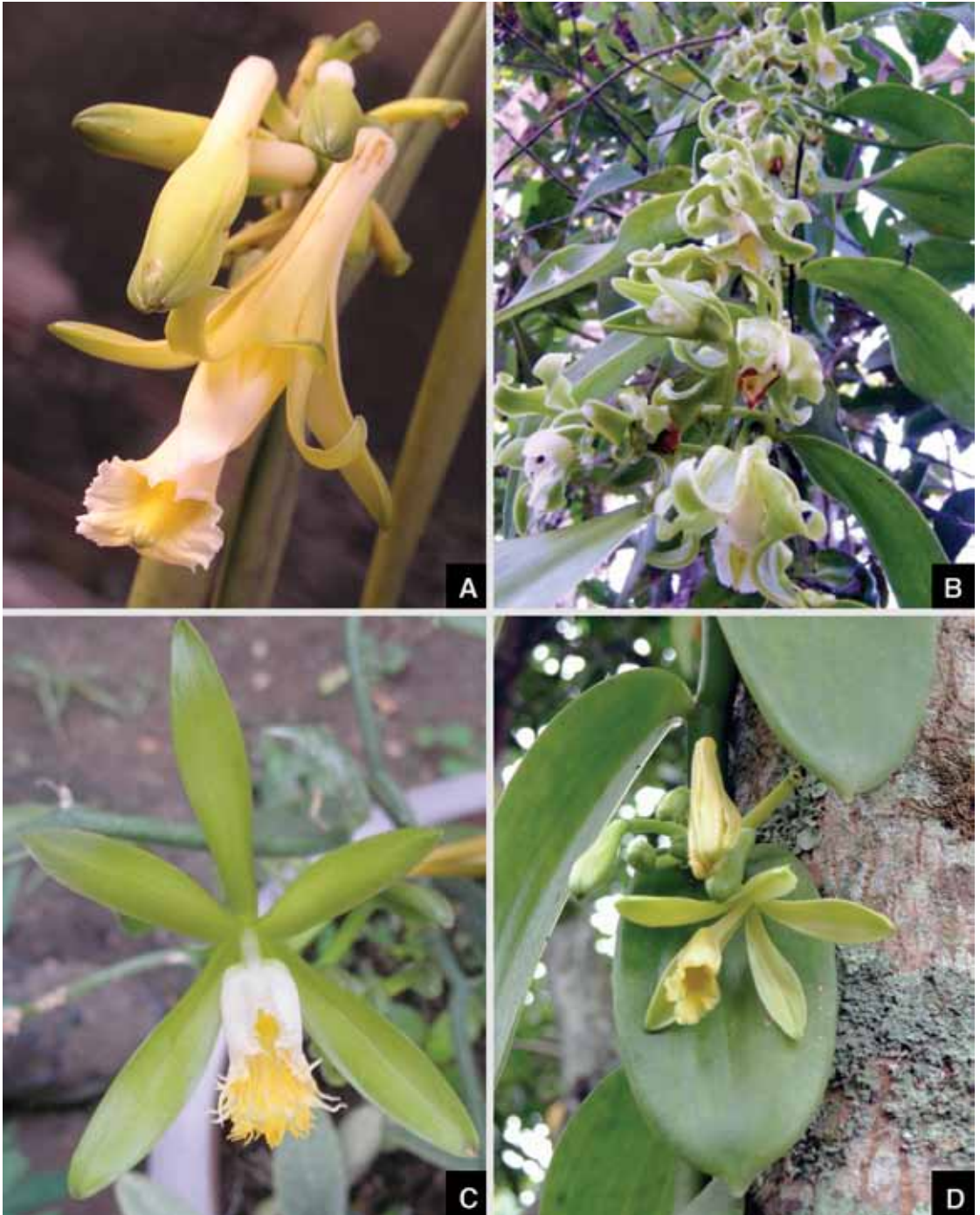


FIGURE 17. A — *Vanilla calyculata*. B — *Vanilla guianensis*. C — *Vanilla insignis*. D — *Vanilla phaeantha*.

Pl. Amer. Genera 25, pl. 28, 1703!

Epidendrum vanilla L., Sp. Pl. ed. 1, 2: 952. 1753.

Lectotype (icon designated by Cribb, Taxon: 48(1): 47. 1999): “*Volubilis siliquosa plantaginis folio*” in Catesby, Nat. Hist. Carolina 2 (3): app. t. 7. 1747.

V. vanilla (L.) Britton in Britton & Wilson, Bot. Porto Rico 5: 185. 1924.

Syn: *V. aromatica* L. (based on the same specimen).

V. aromatica Sw., Nov. Act. Soc. Sc. Upsal. 6: 66. 1799.

TYPE: Haiti, *Plumier s.n.*, the holotype is the original drawing by Plumier.

V. anaromatica Griseb. Fl. Brit. W. Ind. 638. (?)

V. epidendrum Mirbel, Hist. Pl. ed. II. 9: 249. 1802-6.

V. vanilla Karst. Deutsch Fl. ed. 2, 1: 474. 1895.

V. vanilla Huth, Helios 11: 136. 1893.

Vanilla mexicana has been repeatedly cited from Central America because the prevailing confusion between this species and *Vanilla inodora*. In spite of its name, it is a plant from the West Indies and northeastern South America. It is recognized by the large flowers with apple-green tepals and white, distinctly trilobed, 3-keeled lip. Other specimens labeled as *V. mexicana* from Costa Rica belong to the new species here proposed as *V. costaricensis*.

***Vanilla planifolia* Jackson x *V. pompona* Schiede x *V. planifolia* Jackson**

This artificial hybrid was created in Madagascar. It was imported to Costa Rica, where is rather common, and it is said that it is very resistant to root rot disease (David Gardella, com. pers.). ITS sequences are polymorphic and similar to both *V. pompona* subsp. *grandiflora* and to *V. planifolia*. MatK and rbcL sequences are grouped with *V. planifolia* sequences, which suggest that *V. planifolia* was used as the maternal progenitor, since the plastid genome is inherited maternally.

***Vanilla x tahitensis* J.W. Moore, Bishop Mus. Bull. Bot. 102: 25. 1933.**

TYPE: Flora of the Society Islands, Island of

Raiatea, altitude 20 m; on trees, escaped from cultivation; 3rd valley south of Faaroa Bay, 2-3 dm high. Native name *Vanira tahiti*, Nov. 11, 1923, *J.W. Moore 294*, holo. Bernice P. Bishop Museum Herbarium (559503)!

V. hirsuta M.A. Clements & D.L. Jones, Lasianthera 1(1): 47. 1996

TYPE: Papua New Guinea, *M.A. Clements 6742* CANB(holo.) iso(NCBG) not seen, photo!

ADDITIONAL SPECIMENS: FRENCH POLYNESIA: Raiatea: *H. St. Johns 17310* K! Mongareva Is. *H. St. Johns 14459* K(drawing)!

Vanilla tiarei Constantin & bois, Compt. Rend. 1915 161: 202, *nomem*

TYPE: Tahiti.

DISTRIBUTION: Known from French Polynesia (Society Islands), and New Guinea. The Tahitian vanilla certainly is not known in Central America.

Vanilla tahitiensis J.W. Moore was described from material from Raiatea, Society Islands. The type corresponds to the plant widely cultivated in French Polynesia and known as “Vanille de Tahiti”, and the second most important source of commercial vanilla. The same taxon was also recently redescribed by Clements & Jones (1996) as *V. hirsuta*, based on a specimen collected in Papua New Guinea (*M.A. Clements 6742* CANB(holotype), NCBG(isotype) not seen, photos!). There are also other different plants in Tahiti, including *V. planifolia*, and some variants of *V. tahitiensis* that may represent different cultivars or different species (e.g. a plant labeled as cv. Tahita is apparently *V. bahiana*).

Porteres (1954) indicated that the origin of *V. tahitiensis* was very enigmatic. It has been suggested also that the distribution of *V. tahitiensis* is far from other vanillas, that its occurrence in Tahiti is perhaps due to a human introduction, and that it is very similar to *V. planifolia* and not to the species from New Guinea, which is the area with native vanillas closest to Tahiti, such as *V. giulianettii* F.M. Bayley, *V. kaniensis* Schltr., *V. kempteriana* Schltr., *V. ramificans* (J.J. Sm.) J.J. Sm., *V. variensis* Schltr.

Except for *V. tahitiensis*, all the *Vanilla* species with aromatic fruits are restricted to the Neotropics (Soto, 2003). Occasional reports of fragrant fruits in Asia (e.g. Heyne, 1922) are probably based in wrong observations, or in odors unlike the typical vanilla fragrance. *Vanilla*

lineages are confined to particular geographic areas, and disjunctions are better explained by ancient vicariant events than by long distance dispersal (Soto *et al.*, in prep).

Vanilla (in the generic sense) was introduced to Tahiti from Manila about 1848. Pétard (1986: 123) claimed that Admiral Hamelin was responsible for bringing the plants to the Botanic Garden at Papeete, whereas Herman *et al.* (1989: 20) asserted that William Ellis, a missionary from London Missionary Society, brought cuttings from the Philippines (Smith *et al.*, 1992). Ryan (1986) agrees that the origin of *V. tahitiensis* is uncertain, she said that it may be that some *Vanilla planifolia* plant stock was hybridized or that it mutated, allegedly in the Philippines and that *V. tahitiensis* is not native of the South Pacific Islands, but she did not give more data about this statement, although she indicates Tahitian growers as the source of the information.

Morphological variation in *Vanilla planifolia* is rather great, but it is clear that traits exhibited by *V. tahitiensis* depart from the known variation of *V. planifolia*. It is difficult to think of a somatic mutation than could cause such conspicuous differences. Sexual reproduction of vanilla is almost impossible under plantation conditions, and the life span is long enough to discard rapid artificial selection as a probable source of such “novelties”. Therefore, the hybrid hypothesis is more plausible.

The hybrid origin of *V. tahitiensis* was suspected by Portères (1954) and Pétard (1986), who suggested that it arose from a cross between *V. fragrans* (= *V. planifolia*) and *V. pompona*. *Vanilla tahitiensis* is morphologically very similar to *V. planifolia* and its allies, especially *V. odorata* and *V. insignis*, but not to *V. pompona*. The hybrid between [*V. pompona* × *V. planifolia*] × *V. planifolia* has thicker stems, leaves, and different flowers than *V. tahitiensis*.

Compared to *V. planifolia*, *V. tahitiensis* has retrorse warts on the midlobe of the lip. Since this trait is a synapomorphy of the group of *V. odorata* (including *V. odorata*, *V. fimbriata*, *V. helleri*, and *V. insignis*, and also *V. cristagalli* and *V. ribeiroi* from South America), if of hybrid origin one of these taxa is the candidate for parental species in addition to *V. planifolia*. *V. helleri* has a very short lip claw, and widely elliptic leaves, broader than either in *V. planifolia* or *V. tahitiensis*. *V. insignis* has conspicuously sulcate, papillose stems,

and leaves similar in shape to *V. planifolia*. Since *V. tahitiensis* has slender stems, narrower leaves, longer perianth segments and column, the best candidates for a parental species are *V. odorata* and *V. fimbriata* (if this is specifically distinct from *V. odorata*), both with slender stems, narrower leaves, longer perianth segments and column, than *V. planifolia* and *V. tahitiensis*.

Vanilla odorata is an important source of vanilla fruits from the wild. Most vanilla beans collected by peasants in Chiapas, Mexico are from *V. odorata*, since wild *V. planifolia* is extremely rare or absent. Ames also reported that it was the best quality species in Ecuador; and herbarium records from Bolivia indicate that “it was the best one there”. Furthermore, *V. odorata* has some interesting features that make it a good candidate in a *Vanilla* hybridization program, such as the higher tolerance to more open habitats, its origin from places with higher annual rainfall and more equatorial climates, tolerant to occasionally flooded terrains, and its resistance to the attack of “chinche roja” (*Tentecoris confusus*) (M. Soto, pers. observations); nothing is known about its resistance to fungal and bacterial diseases, but it seems not as susceptible as *V. planifolia* (M. Soto, pers. obs.). *Vanilla planifolia* and *V. odorata* may be sympatric in several regions of Central America. In Northern Oaxaca, Mexico, both species have been found intermingled and flowering at the same time. Both species are probably pollinated by Euglossine bees (apparently *Euglossa viridissima* in the case of *V. planifolia*) involving a pollination system involving deception. Fragrance analysis

Vanilla tahitiensis is the only *Vanilla* species from which there are reports of diploid and tetraploid chromosome counts. Tonier (1951) reported 64 somatic chromosomes for “*Vanilla haapape*”(sic), considered to be a variety of *V. tahitiensis* (R. Porterès, 1954), while Heftimiu-Heim (1941) reported 2n=32 for *V. tahiti* (sic) and *V. papeno* (sic), the later a common name of *V. tahitiensis* var. *haapape* (Porterès *op. cit.*).

ITS sequences of a specimen of *V. tahitiensis* cultivated in France, and another gathered from the Gene Bank as *V. hirsuta* are nested into one of the clades of *V. odorata* with 100% of bootstrap support (other specimens of *V. odorata* have an ITS sequence more similar to that of *V. helleri*).

Although we do not have flowering material of *V. tahitiensis* to make a quantitative analysis of the

intermediate morphology character of it between *V. planifolia* and *V. odorata*, qualitative data support the hybrid origin between these species. ITS sequences indicate an extremely close relationship with *V. odorata*. However, Schlüter found that was no evidence of a hybrid origin analysing.

In conclusion, it is suggested that *V. tahitensis* is a taxon of hybrid origin between *V. odorata* and *V. planifolia* introduced to Tahiti from Phillipines. Lubinsky *et al.* (2008) provide strong support for the hybrid origin of *V. tahitensis* from cross(es) of *V. planifolia* and *V. odorata*. It is not improbable that this cross was taken from Mexico to the Philippines when both countries were ruled by the Spanish crown and subject to a large commercial exchange thanks to the Manila Galleon, that connected Acapulco with the far east. The large variation observed (Maurice Wong, pers. com.) and detected by RAPDs in the tahitian vanilla is an additional point that supports its hybrid origin. Lubinsky *et al.* (2008) have suggested that *V. x tahitensis* can be an artificial hybrid and even postulated a postclassic origin. Orchid hybridization and subsequent germination of the sclerotic seeds is almost impossible under primitive conditions. Even now, *Vanilla* seeds are planted from immature fruits in which the testa have not become hard and it is thought that mature seeds in ripe fruits must pass through the digestive tract of a bat to germinate under natural conditions. Given the sympatricity of *V. planifolia* and *V. odorata*, the same flowering season, and the prevalence of the similar herbal aroma with cinnamon-like notes in both species, is not unlikely that they share the same pollinator, apparently *Euglossa viridissima* in *V. planifolia*. Therefore, a spontaneous hybrid between *V. planifolia* and *V. odorata* may be the source of *V. x tahitensis*, with a later selfing or back-crossing with *V. planifolia*, already in Tahiti, that gave origin to the variation in cultivars, genotypes and chromosomic numbers.

The following specimens are sterile, but their leaf morphology is so different to the rest of the Central American *Vanilla*, that we are convinced that they represent a different, undescribed species. The leaves are rather thin, but not as thin as those of subsect. *Membranacea*; the leaves are conspicuously obovate and abruptly mucronate.

COSTA RICA: CARTAGO: Sin flores ni frutos, Instituto [Interamericano de Ciencias Agrícolas], Turrialba, en el bosque, 600 m alt., 23-VIII-49, *J. Léon 1692* US(2021492)!
GUANACASTE: Large epiphytic vine in moist forest, El Silencio, near Tilarán, altitude about 750 m, Jan. 13, 1926, *P.C. Standley & J. Valerio 44791* US(1309513)!

There are very few records on vanilla dispersal, but bat dispersal had been suggested in *V. insignis* (M. Soto, unpublished data) and recently observed in *V. pompona* (N. Byrd, pers. com.). Bird dispersal is expected in some Asian species, as *V. abundiflora* J.J. Smith and *V. griffithii* Rehb. f., and also in the closely related genera *Cyrtosia*.

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A NEW INFRAGENERIC CLASSIFICATION AND SYNOPSIS OF THE GENUS *VANILLA* PLUM. EX MILL. (ORCHIDACEAE: VANILLINAE)

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ABSTRACT. An updated, annotated checklist of the species of the genus *Vanilla* is presented, with information on nomenclature, distribution, literature and examined specimens. A key for the determination of the species is included. A new proposal of infrageneric classification of *Vanilla* is provided.

RESUMEN. Se presenta un listado actualizado, comentado de las especies del género *Vanilla*, donde se proporciona información nomenclatural, distribucional, literatura y especímenes examinados. Se incluye una clave para la determinación de las especies. Finalmente se presenta una nueva propuesta de la clasificación infragenerica de *Vanilla*.

KEY WORDS / PALABRAS CLAVE: Orchidaceae, *Vanilla*, checklist, listado, infrageneric classification, clasificación infragenerica

The pantropical genus *Vanilla* Plum. ex Mill. belongs to the subtribe Vanillinae and the subfamily Vanilleae, it comprises some 106 species of hemiepiphytic vinous orchids (Soto Arenas, 2003). Recent phylogenetic analyses have shown that it is closely related to the South American genera *Dictyophyllaria* Garay and *Epistephium* Kunth and to the achlorophyllous genus *Lecanorchis* Blume (Cameron, 1996; Cameron *et al.*, 1999, Soto Arenas & Alvarez-Buylla, in press).

Information on vanillas has been collected for a phylogenetic analysis, but since no modern revision exists, it has been necessary to evaluate the status of all the proposed taxa. The results of this survey are presented here, pending the production a formal revision.

Vanilla has proved to be a taxonomically difficult genus (Soto Arenas, 2003). The first species were named before the establishment of the binomial system of nomenclature (Linnaeus, 1753) and their nomenclature and typification is confusing. Some taxa were described from sterile material, and like other hemiepiphytic plants, vegetative traits vary greatly, rendering such characters difficult to use for determination. A particular problem is that several taxa have been described from immature buds, in

which measurements, and shape of the segments can be substantially different from the morphology of the same features at anthesis, making identification uncertain. Furthermore, numerous species are known from a surprisingly small number of specimens, mostly due to the scarcity of available flowering material because of their irregular flowering and the ephemeral nature of the flowers, the positioning of the inflorescences in the canopy of the rain forests, and the low density of some populations. Vanillas from densely populated areas in the tropics apparently face severe conservation problems and their populations are often depleted. Additional complications are the poor preservation of the flowers in herbarium specimens, the flowers often rotting before they dry, and the presence of some complexes in which interspecific differentiation is subtle. A very large group of American species is pollinated by male Euglossine bees attracted by chemical compounds (Roubik and Ackerman, 1987; Dressler 1993; Soto Arenas & Alvarez-Buylla, pers. obs.). In other orchids with similar pollination systems, there may there be little morphological differentiation, yet the species can be effectively separated by barriers imposed by the fragrance-

collecting behavior of their pollinators (van der Pijl & Dodson 1966).

Our knowledge of *Vanilla* is therefore far from adequate to produce a good, modern revision of the group, although there have been important contributions, such as two revisions of *Vanilla* (Rolfe, 1896; Portères, 1954), the treatment by Klotzsch (1845) and regional accounts by Hoehne (1945), Correll (1951), Cribb & Hunt (1984), La Croix & Cribb (1995), Luer (1972), Summerhayes (1968), Seidenfaden (1992), and Szlachetko and Olzewski (1999). The revision by Portères, the last full account of the genus, although useful, is somewhat out-of-date because, although we accept a similar number of species in this checklist compared with his revision (110 species), there are substantial differences. The description of several new species, improved collections of some poorly-known taxa clarifying their status, and our understanding of the distribution of the species and their phylogenetic relationships (Soto Arenas, 2003; Soto Arenas *et al.*, unpublished results) have improved our understanding of the genus.

The fragmentary or poor material of some taxa available to Portères (1954) led him to propose affinities between taxa that belong to different lineages of the group. Therefore, the aims of this paper are to present a new classification of the genus based on cladistic analysis of morphological and molecular data presented elsewhere (Soto Arenas, 2003; Soto Arenas & Alvarez-Buylla, in press), to present an updated checklist of the species and to stress where more information is needed. This revision will also allow the better identification of species and constitute a base for future research.

Material and methods

A bibliographic revision was conducted. Specimens were examined in the following herbaria: AMES, AMO, BM, F, G, K, L, NY, P, W. Special attention was paid to type and critical specimens, for example flowering material from type localities where the species were described from sterile or immature material. When possible, we examined cultivated and living wild specimens, spirit-preserved flowers, botanical illustrations and photographs. Affinities of many taxa have been assessed with the aid of

molecular data, published elsewhere (Soto Arenas, 2003; Soto Arenas *et al.*, in press).

Infrageneric classification of *Vanilla*

The genus *Vanilla* is a rather diverse assemblage of species of pantropical distribution. Despite the lack of morphological synapomorphies in the genus, there is strong molecular evidence that it is monophyletic (Soto Arenas & Alvarez-Buylla, in prep., Cameron, unpubl. data). The following combination of characters are diagnostic for *Vanilla*: the hemiepiphytic vinous monopodial growth habit, with roots produced at each internode (these characters are found in some Galeolinae, a subtribe that may be considered part of Vanillinae, and *Clemastepistephium* N.Hallé), fleshy fruits and the wingless seeds with a hard seed coat (similar seeds are apparently found in *Dictyophyllaria*).

Vanilla is an ancient group, and most morphological groups within it are monophyletic and have defined geographic distributions. In many ways it is a very diverse genus compared with others in the Orchidaceae. Some authors might favor the idea that the genus should be split into more uniform assemblages with a more restricted geographic distribution. The type species, *Vanilla mexicana*, and most of Portères' section *Membranacea* could be easily considered as the genus *Vanilla* with the rest of the species separated in a different genus. Strong molecular and morphological information supports this view, although it is equally correct (in terms of recognizing monophyletic taxa) to consider all of them in a single genus, although it has few morphological synapomorphies.

The inner lineages of the genus may be supported by molecular characters, but most of them lack morphological synapomorphies that permit their recognition and we found that their acceptance as separate genera is not favoured by other authors. One of the main reasons to keep *Vanilla* in its traditional sense is to keep the traditional use of the name. The type species, *V. mexicana*, is in one of the two main clades, and the species cultivated for their aromatic fruits fall in the other one. To recognize both lineages as different genera would produce the following problems:

- The proposal of a new genus to accommodate the economically most important species in the

Orchidaceae, to which the name “vanilla” or “vainilla” has been attached since pre-Linnean times.

- A new lectotypification of the genus, whose nomenclature has been historically complex, and conservation of the name for the cultivated species.

We believe that to keep *Vanilla* in its traditional sense is congruent with the phylogeny of the group and to maintain the nomenclatural stability that has now been reached.

Rolfe (1896) proposed a formal infrageneric classification of *Vanilla*, recognising two sections: *Foliosae* and *Aphyllae*. Portères (1954) accepted Rolfe’s sections and, in *Foliosae*, proposed 3 subsections: *Papillosae*, *Lamellosae* and *Membranacea*. However, his subsections are invalid as he provided them with neither a Latin diagnosis nor a type. Furthermore, his sections and subsections are polyphyletic, except for subsection *Membranacea* which is paraphyletic (Soto Arenas, 2003).

Section *Aphyllae* is polyphyletic, because the leafless habit evolved independently at least four times in the genus, or maybe is the plesiomorphic condition for the clade containing the Caribbean-Paleotropical taxa, in which leafy species are also included. The leafless condition evolved independently at least once (*V. penicillata*) in the clade of *V. planifolia*. If sect. *Aphyllae* is polyphyletic, then sect. *Foliosae* is also polyphyletic. These sections are also hierarchically incongruent, because they do not reveal the existence of the two main clades in the genus: the membranaceous species and all the others. Porterés included both *V. wrightii* (= *V. bicolor*) and *V. palmarum*, the most basal species in the clade containing the American non-membranaceous leafy species, and *V. weberbaueriana* (= *V. ruiziana*) and *V. pleei*, to which he had no access to appropriate material (see comments under these species in the checklist) in subsect. *Membranacea*. Subsections *Papillosae* and *Lamellosae* are very heterogeneous and incongruent with our cladistic analyses.

In order to be congruent with the phylogenetic analyses, we propose *Vanilla* to be formed by two subgenera: *Vanilla* and *Xanata*. As defined here subgenus *Xanata* comprises two sections: *Xanata* and *Tethya*.

Proposed classification of *Vanilla*

The following classification is proposed here. Species groups are indicated in an informal way. They are easily recognized morphologically, but there is little evidence of their monophyly, and in some cases they may well be paraphyletic.

A. *Vanilla* subgenus *Vanilla*

Vanilla subsect. *Membranacea* Portères in Bouriquet, Le Vanillier et La Vanille: 159 (1959). *nom. illeg.*

Plants with membranaceous leaves. Inflorescences scarcely or not at all differentiated from vegetative axis. Lip without a penicillate callus. Column united to the lip only at the base. Column with a subperpendicular, protruding anther (incumbent only 90°), concave stigma, and smooth ventral surface. Type species: *V. mexicana* Mill.

DISTRIBUTION: 15 species in the Neotropics, most diverse in southern Brazil.

Subgenus *Vanilla* has never been used as a name for this taxon, but it is automatically applicable to the group of *V. mexicana* Mill., the type species of the genus.

The genus *Dictyophyllaria* is practically identical in floral morphology to the *V. parvifolia* group. Its recollection and comparison with this subgenus and other Vanillinae is much needed.

Two groups can be recognized, but their limits are not clear-cut:

1. ***V. mexicana* group:** Petals undulate; sepals usually inrolled; lip very wide, 3- to 5-lobed, with a wide, obtuse apical lobe and numerous high keels or an elevated, very fleshy callus; and column lacking a basal triangular keel on the abaxial surface.

Species placed here include *Vanilla costaricensis*, *V. guianensis*, *V. inodora*, *V. martinezii*, *V. methonica*, *V. mexicana*, *V. oroana* and *V. ovata*.

2. ***V. parviflora* group:** Petals not undulate; sepals not inrolled; lip 3-lobed, with a rounded-quadrate apical lobe, a blade with axial rows of warts; and column with a basal triangular keel on the abaxial surface.

Species included here are *V. angustipetala*, *V. parvifolia* and *V. verrucosa*. Similar to these, but flowers larger with smooth keels, and an acuminate

midlobe of the lip are *V. bertonensis*, *V. bradei*, *V. edwallii* and *V. organensis*.

B. *Vanilla* subgenus *Xanata* Soto Arenas & Cribb **subgen. nov.** a sectione typica plantis foliosis vel aphyllis; inflorescentiis elongatis ab surculo vegetato valde differt; callo penicillato labelli deficienti; columna ad labello medio adnata, latus adaxialis glaber vel pubescens; anthera ventralis ad columna parallela; lobis stigmatibus emergentibus distinguenda.

Typus: *Vanilla planifolia* G. Jackson.

Plants leafy or leafless. Leaves coriaceous-fleshy. Inflorescence a specialized axis, very different from vegetative ones. Lip with or lacking a penicillate callus. Column united to the lip usually more than a half of its length. Column with a parallel, somewhat ventral anther, emergent stigmatic lobes, and with a smooth or often hairy ventral surface.

DISTRIBUTION: pantropical.

DERIVATION OF THE NAME: from the Mexican Indian Totonaco name for *Vanilla*, “xanat” or “shanat”. Totonaco Indians are thought to have brought *Vanilla planifolia* to cultivation.

a. *Vanilla* subgen. *Xanata* sect. *Xanata*

3. *Vanilla palmarum* group: Ovaries calyculate; flowers without a penicillate callus; lip rather entire and united to the column only about a half of column length, with longitudinal pubescent to hirsute lines on the distal half of the lip.

DISTRIBUTION: West Indies and South America.

Species included here are *V. bicolor*, *V. palmarum* and *V. savannarum*.

4. *V. trigonocarpa* group: Lip very inflated with much crenulate margins; vegetative habit mesophytic; racemes few-flowered; flowers very fragrant, small to huge; fruit trigonous, very long and fleshy. Probably a grade rather than a clade.

DISTRIBUTION: Tropical America, from Costa Rica to Amazonia.

Species included here are *V. espondeae*, *V. hartii*, *V. sprucei* and *V. trigonocarpa*.

5. *V. planifolia* group: Flowers greenish; lip concave and with small papillae in the apical region. The South American species have an apical callus connected with the penicillate callus in the middle of the lip by rows of papillae and with the lip apex usually recurved

DISTRIBUTION: Widespread in Tropical America, including the West Indies.

Species included here are *V. appendiculata*, *V. bahiana*, *V. cristagalli*, *V. denticulata*, *V. dubia*, *V. dungsii*, *V. fimbriata*, *V. helleri*, *V. insignis*, *V. odorata*, *V. phaeantha*, *V. planifolia*, *V. ribeiroi*, *V. schwackeana*, *V. tahitiensis* and *V. uncinata*.

6. *V. penicillata* group: Plants leafless, but related to the American leafy, penicillate species. Petals subunguiculate, lip long-unguiculate, with penicillate callus, and villose apex. Fruit calyculate. Similar to the leafy *V. ribeiroi* and, except by the leafless condition, belonging to the *V. planifolia* group.

DISTRIBUTION: Guyana-Amazonia.

The only species included here is *V. penicillata*.

7. *V. hostmanii* group: Flowers large, usually white with a yellow-orange lip; lip with thickened, radiating veins on the distal half that can be somewhat warty (the warts rounded and flattened); inflorescences with rather distichous bracts; Ovary, sepals, and petals granulose keeled, very conspicuously so in some species; Lip surface puberulent-cellular-papillose in some species; perianth segments sometimes with crystal druses included.

DISTRIBUTION: Widespread in Tropical America, except for the West Indies.

Species included here are *V. cribbiana*, *V. dressleri*, *V. gardneri*, *V. hostmannii* and *V. ruiziana*.

8. *V. pompona* group: Leaves very fleshy; stems thick, xerophytic; lip rather smooth, except for the penicillate callus, and with a slightly thickened axial cushion running from the penicillate callus to the apex; flowers strongly fragrant, yellow with an orange lip; fruits thick, trigonous, banana-like.

DISTRIBUTION: Widespread in Tropical America, except for the West Indies.

Species included here are *V. calyculata*, *V.*

chamissonis, *V. columbiana*, *V. grandiflora*, *V. pompona*, *V. pseudopompona* and *V. vellozii*.

b. *Vanilla* subgen *Xanata* sect. *Tethya* Soto Arenas & Cribb, **sect. nov.** a sectione *Xanata* foliis absentibus vel praesentibus, carnosius vel coriaceis; ovario non calycoso; floribus saepe labelli callo penicillato ornatis; labello manifeste vel obscure trilobato, ad columnam liberato, in partem apicalem lineis pubescentibus destituta distinguenda.

Typus: *Vanilla phalaenopsis* Rchb. f. ex van Houtte.

DERIVATION OF THE NAME: From the ancient Tethys Sea, thought to be the migration route of *Vanilla* into the Palaetropics.

9. ***V. kinabaluensis* group:** Leaves usually very broad, elliptic; stems terete; inflorescences multi-flowered, in some species with up to 150 flowers (*V. abundiflora* and *V. kinabaluensis*); ovary stout, especially in New Guinean species; fruit thick and relatively short; tepals concolorous, greenish-yellowish, usually obtuse; lip cuneate or cuneate-flabellate in some New Guinean species, trumpet-shaped, not unguiculate, more or less trilobed, with the midlobe often recurved and with rows of reddish subulate papillae that may be very long and flattened in *V. kinabaluensis*, or whitish and longer in *V. siamensis*. Most species of this group are seldom collected and many are imperfectly known, but several of them seem to be closely related or maybe conspecific. The group is much more developed in the Malay Archipelago and New Guinea.

DISTRIBUTION: From S China to New Guinea, most abundant in Indonesia.

Species included here are *V. abundiflora*, *V. giullianetii*, *V. kaniensis*, *V. kempteriana*, *V. kinabaluensis*, *V. klabatiensis*, *V. ovalis*, *V. platyphylla*, *V. ramificans*, *V. siamensis*, *V. seranica*, *V. sumatrana*, *V. utteridgei* and *V. wariensis*.

10. ***V. albida* group:** An Asiatic group with flowers and plants similar in appearance to the American *V. planifolia* group; flowers greenish white; lip long-unguiculate; tepals long; and lip with short apical papillae. Some species, such as *V. moonii* and *V. yersiniana*, and perhaps others have sulcate stems in the way of *V. insignis*. *V. albida*, *V. andamanica*,

V. montana and *V. yersiniana* are closely related, differing in morphological details and distribution. *V. havilandii* seems to belong here, but has a very different inflorescence, bearing very small flowers. *V. moonii* has buff-colored tepals and yellow lip with apical papillae arranged in two rows, representing perhaps a shared character with *V. annamica* and *V. somai*.

DISTRIBUTION: Sri Lanka to SE Asia and the Malay Archipelago across to Borneo.

Species included here are *V. albida*, *V. andamanica*, *V. havilandii*, *V. montana*, *V. moonii*, *V. sanjappae* and *V. yersiniana*.

11. ***V. annamica* group:** Inflorescences very distinct, paniculate, bearing biflorous cymes; flowers trumpet-shaped; and the lip has two apical, parallel rows of papillae.

DISTRIBUTION: S China, Taiwan and Indochina.

Species included here are *V. annamica* and *V. somai*.

12. ***V. griffithii* group:** *V. palembanica* is very imperfectly known, but it seems to be allied to *V. griffithii*. Leaves broadly elliptic; flowers with very obtuse tepals, a lip with a deeply retuse midlobe, woolly rather than scaly penicillate callus, and truncate buds.

DISTRIBUTION: Sumatra, Borneo and peninsular Malaysia.

Species included here are *V. griffithii* and *V. palembanica*.

13. ***V. borneensis* group:** Callus penicillate, continuous with the pilose lip apex; plants with small, narrow leaves and short inflorescences; lip with a pair of corpuscles at base. They seem to be leafy versions of the *V. aphylla*-*V. calopogon*-*V. wightii* group.

DISTRIBUTION: From India and SE Asia to Indonesia.

Species included here are *V. borneensis* and *V. diabolica*.

14. ***V. imperialis* group:** Flowers large; lip trumpet-shaped, similar to that of the *V. planifolia* group but shorter; callus absent; lip apex papillate.

DISTRIBUTION: Continental Africa.

Species included here are *V. grandifolia*, *V. imperialis*, *V. ochyrae* and *V. polylepis*.

15. ***V. françoisii* group:** Flowers very small, whitish green with the lip rose-tinted at the base and with purple margins; lip entire or six-lobed, densely covered with fleshy hairs or papillae in middle and front.

DISTRIBUTION: Madagascar.

Species included here are *V. françoisii* and *V. coursii*.

16. ***V. chaltotii* group:** Lip sacciform; midlobe reduced, recurved; side lobes well developed.

DISTRIBUTION: West and equatorial Africa.

Species included here are *V. chaltotii*, *V. nigerica* and *V. seretii*.

17. ***V. africana* group:** Lip not sacciform; side lobes of lip united to the basal 1/2-2/3 of the column and forming deep sinuses with the mid-lobe; callus formed by scales or warts; column apex exposed.

DISTRIBUTION: West and equatorial Africa, with a single species in Eastern Africa.

Species included here are *V. acuminata*, *V. africana*,

V. crenulata, *V. cucullata*, *V. hallei*, *V. heterolopha*, *V. ramosa* and *V. zanzibarica*.

18. ***V. barbellata* group:** Flowers green to greenish with a reddish-purplish lip; callus incipient, penicillate.

DISTRIBUTION: Caribbean.

Species included here are *V. bakeri*, *V. barbellata*, *V. claviculata*, *V. dilloniana* and *V. poitaei*.

19. ***V. aphylla* group:** Lip with very long trichomes and sometimes an incipient penicillate callus. Scarcely different from *V. borneensis* group, except for the lack of leaves.

DISTRIBUTION: India to the Philippines.

Species included here are *V. aphylla*, *V. calopogon* and *V. wightii*.

20. ***V. phalaenopsis* group:** Lip flabellate with two rows of hairs besides the axial line; petals obtuse, very wide.

DISTRIBUTION: Indian Ocean basin (East Africa, Comores, Mascarene Islands, Madagascar, with a single species in Sri Lanka and S India).

Species included here are *Vanilla decaryana*, *V. humblotii*, *V. madagascariensis*, *V. phalaenopsis*, *V. perrieri*, *V. roscheri* and *V. walkeriae*.

KEY TO VANILLA

1. Plants leafless, sometimes the new stems bearing small scars or short leaves (much shorter than the internodes, fugaceous and absent in older stems, bracts of the inflorescence **Key I**
1. Plants leafy, the blades well-developed and persisting several years, bracts persistent until the fruit ripens 2
2. Leaves soft, membranous, very thin in herbarium specimens; lip margins united to the column only at base for less than 4 mm; penicillate callus absent **Key II**
2. Leaves coriaceous, fleshy, often chartaceous in dry condition; lip margins united to the column more than 1/3 of column length, usually for more than 8 mm; penicillate callus absent, wanting or often present 3
3. Lip deeply saccate at base **Key III**
3. Lip not saccate at the base 4
4. Stem 4 mm in diameter; leaves very small, 2 cm or less long, much shorter than the internodes 5
4. Stem stouter, 5 mm or more in diameter; leaves much larger, usually more or less as long as the internodes or longer 6
5. Lip side lobes lacerate or deeply erose on front margin, the central callus on lip circular, densely papillate, the mid-lobe of lip densely papillate *V. penicillata*
5. Lip crenulate towards apex, the disc densely hairy *V. françoisii*
6. Lip hexagonal in outline *V. coursii*

6. Lip entire to 3-lobed 7
7. Lip 3-lobed in basal half **Key IV**
7. Lip entire or 3-lobed in apical half 8
8. Inflorescence paniculate, each branch a 2-flowered cyme 9
8. Inflorescence racemose or, if branched, then branches not 2-flowered 11
9. Lip hexagonal *V. coursii*
9. Lip not hexagonal 10
10. Lip entire, broadest in middle, callus densely papillose, running from base of lip almost to tip *V. annamica*
10. Lip 3-lobed, broadest across the apex; callus on disc, elongate-elliptic, papillose, with a few scattered papillae on the mid-lobe *V. somai*
11. Lip disc lacking a central almost quadrate tuft of erose or lacerate callus; callus papillose, hairy or of several erose or papillose ridges running the length of the lip **Key V**
11. Lip with a central tufted or convex callus 12
12. Lip cuneate or cuneate-flabellate, lacking a prominently narrowed claw when spread flat, usually 1.5 times as long as broad or less; species from Old World **Key VI**
12. Lip with a prominent narrowed claw when spread; lip usually more than 1.5 times as long as broad **Key VII**

KEY I

1. Inflorescences subcorymbose, very long; bracts deciduous; flowers white, yellow or greenish with pink or maroon blotches deep in the throat of the lip; petals much broader than sepals; penicillate callus absent, but with rows of longitudinal papillae; species from the Indian Ocean basin: E Africa, Madagascar, Sri-Lanka, India, Seychelles, Comoros 2
1. Inflorescences racemose; flowers greenish-white, often flushed or blotched with purple; lip with a penicillate callus and other trichomes towards the apex; species from America 8
2. Column of 14-17 mm long; sepals 25-30 mm long *V. decaryana*
2. Column 18-30 mm long; sepals 50-70 mm long 3
3. Flowers white with a yellow throat; veins of the petals and lip thin, almost straight *V. walkerae*
3. Flowers white with an apricot or pink throat or yellow with orange or maroon markings in the throat of the lip; veins of the petals and lip partially or totally sinuous-undulate 4
4. Column 27-30 mm; lip covered with long, scattered hairs in the middle, veins slightly flexuous in the petals and the upper half of the lip; flowers yellow with the throat of the lip maroon or orange 5
4. Column 18-23 mm; disc of the lip adorned with 2 lines of long papillae or fleshy hairs; veins of the petals and lip all very sinuous-flexuous; flowers white, the lip a pink-reddish blotch on the throat 6
5. Lip papillose; column 20 mm long *V. humblottii*
5. Lip not papillose; column 27-30 mm long *V. perrieri*
6. Sepals 75-80 mm long; stem 12-20 mm in diamet. *V. roscheri*
6. Sepals 50-65 mm long; stem 8-10 mm in diam. 7
7. Lip oblong, acute, the margins undulate *V. phalaenopsis*
7. Lip obovate, obtuse, the margins not undulate *V. madagascariensis*
8. Stems slender, usually less than 5 mm in diam. when mature in living condition; penicillate callus well-defined; column fused to the lip margins until stigmatic region; margins of the obscure lateral lobes of the lip lacerate-fimbriate, lip more than 50 mm long; Amazonian plants *V. penicillata*
8. Stems thick, about 1 cm or more in diam. when mature in living condition; lip less than 50 mm long; lip apical margins crenulate, undulate or entire, not lacerate-fimbriate; Caribbean plants 9
9. Leaf present at each internode, persistent, to half or more the length of the internode, leaves plane, apices hooked; lip green with maroon margin and veins, hairs yellow, margins irregular *V. poitaei*

9. Leaves not present at each internode, most or early deciduous, usually much less than half the length of the internode, leaf margin at least somewhat revolute, apices straight, curved, or hooked; lip not colored as above, margins more or less entire 10
10. Lip entire, broadly rounded at apex, with simple or forked flattened hairs along longitudinal rows in the middle of the lip to the apex, stem squarish *V. claviculata*
10. Lip shallowly or deeply 3-lobed, without scale-like or flattened hairs to the lip apex 11
11. Lip less than 4 cm long, deeply 3-lobed at the truncate apex, with sinuses prominent *V. barbellata*
11. Lip more than 4 cm long, broadly rounded above with a projecting apical lobe, without distinct *V. dilloniana*

KEY II

1. Tepals contorted; flowers medium to large sized; lip 30 mm or more long, 3-lobed or entire 2
1. Tepals not contorted but occasionally slightly undulate; flowers small; lip less than 30 mm long, neatly 3-lobed 13
2. Lip entire, pentagonal or hexagonal 3
2. Lip 3-lobed 4
3. Lip < 5 cm long, with basal, warty keels, species from Guatemala *V. martinezii*
3. Lip > 5 cm long, basal veins of the lip smooth, species from Amazonia and Guyanas *V. guianensis*
4. Midlobe of the lip strongly emarginate 5
4. Midlobe of the lip broadly elliptic, ovate, subquadrate 7
5. Lip with a high, axial, fleshy, cushion-like callus *V. inodora*
5. Lip with 3-keeled callus, converging and thickened and rugose near the apex 6
6. Bracts small, 5.0-7.5 mm long; lip not papillose *V. methonica*
6. Bracts foliaceous, 110-150 × 65-71.5 mm; lip papillose *V. oroana*
7. Midlobe of the lip triangular, elongate, acuminate 8
7. Midlobe of the lip not conspicuously emarginate, acute, truncate or obtuse 11
8. Fertile bracts foliaceous 9
8. Fertile bracts not foliaceous 10
9. Lip distinctly 3-lobed, 29 mm long *V. bradei*
9. Lip obscurely 3-lobed, 30-37 mm long *V. organensis*
10. Leaves 7-8 cm broad; column 25 mm long *V. acuta*
10. Leaves 5-7 cm broad; column 20-25 mm long *V. bertonienensis*
11. Midlobe of the lip very short, quadrate, truncate, scarcely extending beyond the lateral ones *V. costaricensis*
11. Midlobe of the lip ovate-elliptic, conspicuously longer than the lateral ones 12
12. Petals > 40 mm long *V. mexicana*
12. Petals < 38 mm long *V. ovata*
13. Lip with longitudinal, smooth keels, lacking papillae *V. parvifolia*
13. Lip with rows of papillae and keels 14
14. Lip 20 mm long *V. verrucosa*
14. Lip 23-29.5 mm long *V. angustipetala*

KEY III

1. Flowers small; sepals < 22 mm long; lip conspicuously 3-lobed, the midlobe very short and recurved *V. chalcotii*
1. Flowers large; sepals > 34 mm long; lip obscurely 3-lobed, the midlobe very broad; stems papillose-verrucose 2
2. Lip midlobe strongly recurved-inrolled, the base saccate but without 2 gibbae, the throat slightly hairy. *V. sereti*
2. Lip midlobe recurved, but not rolled, the base with 2 gibbae, the throat densely and coarsely hairy *V. nigerica*

KEY IV

1. Lip mid-lobe deeply emarginate with a fleshy inverted U-shaped callus around the sinus; callus on disc papillose; column straight; lip margins united to column in basal third only; species from Asia *V. griffithii*
1. Lip apical lobe acute or truncate; lip callus not papillose; column strongly arcuate; lip margins united to the column for only 2/3 of column length or less, leaving the column apex very exposed; species of continental Africa 2
2. Lip lacking a penicillate callus, but with a warty axial zone 3
2. Lip with a penicillate callus with scales, not warty, rather thin in substance 4
3. Midlobe of the lip truncate, broader towards the apex *V. heterolopha*
3. Midlobe of the lip acute to acuminate, broader towards the base, thick, fleshy; callus tuberculate, fleshy, half length of midlobe *V. hallei*
4. Leaves small, long cuspidate; raceme dense, simple; midlobe of the lip oblong or obovate-elliptic, not axially thickened on the lower half; callus a tuft of raised toothed crests 5
4. Leaves large, elliptic, acuminate; raceme lax to subdense, simple or branched 6
5. Mid-lobe of the lip oblong or obovate-elliptic, not axially thickened on the lower half
V. africana
5. Mid-lobe of the lip oblong-elliptic, with an axial, thickened keel in the basal half *V. cucullata*
6. Basal bracts of the inflorescence leaf-like, usually broadly elliptic to suborbicular; inflorescence usually simple; lip blade strongly gibbose-conduplicate, with a penicillate callus at the top of the gibba *V. crenulata*
6. Basal bracts of the inflorescence inconspicuous, scale-like; inflorescence simple or branched 7
7. Lip blade slightly gibbose, strongly apiculate at tip; leaves elliptic to very broadly elliptic; species from Kenya, Tanzania, Uganda *V. zanzibarica*
7. Lip blade not gibbose, lip obtuse, apiculate; leaves oblong to elliptic; species from western Africa *V. acuminata*

KEY V

1. Lip callus a more or less circular papillose mound; lip mid-lobe deeply emarginated, the margins of the sinus swollen into a U-shaped callus *V. griffithii*
1. Lip not as above 2
2. Lip central callus of long fine hairs, mid-lobe covered with long fine hairs *V. sanjappae*
2. Lip central callus elongate-oblong, of papillae, dendritic hairs of irregularly lacerate low ridges; mid-lobe of papillae, ridges or glabrous 3
3. Leaves oblong-elliptic, up to 21 cm long and 8 cm broad, rather succulent; floral bracts less than 1.5 cm *V. polylepis*
3. Leaves elliptic to subcircular; floral bracts more than 1.5 cm long 4
4. Inflorescence not closely imbricate, leaves more than 30 cm long, very thin-membranaceous in dried specimens *V. grandifolia*
4. Inflorescence bracts closely imbricate (*Costus*-like); leaves less than 25 cm long 5
5. Lip apex triangular *V. imperialis*
5. Lip apex elliptic to semi-circular *V. ochryae*

KEY VI

1. Inflorescences simple, elongate, usually as long as or longer than the leaves, up to 200-flowered; flowers cream with reddish blotch at the lip apex 2
1. Inflorescences not as many-flowered as above, shorter than the leaves 4
2. Lip 3-lobed, broadest in middle when flattened; mid-lobe of lip with a papillate longitudinal central ridge
..... *V. sumatrana*

2. Lip almost entire, cuneate; mid-lobe of lip lacking a longitudinal papillate ridge 3
3. Column with dendritic hairs below stigma; apex of lip with a horseshoe shaped callus with a lacerate margin *V. abundiflora*
3. Column glabrous; apex of lip with a V-shaped callus of papillae *V. kinabaluensis*
4. Inflorescence branched, leaves oblong, small, < 10 cm long *V. ramificans*
4. Inflorescence simple, leaves usually ovate-elliptic, often very large (e.g. 20 cm long) 5
5. Flowers with yellow-throated lip, apical papillae conspicuous, flattened *V. siamensis*
5. Flowers conspicuously purple-red blotched on the lip, at least in the papillae area 6
6. Lip cuneate-flabellate, not or obscurely 3-lobed, species from New Guinea only 7
6. Lip cuneate, neatly 3-lobed, species from Philippines to Moluccas and New Guinea 11
7. Lip with a pair of rounded calli at the base *V. diabolica*
7. Lip lacking any basal corpuscular calli 8
8. Column hairy on ventral surface facing the lip *V. utteridgei*
8. Column glabrous 9
9. Lip apical margins lacerate-irregularly erose *V. kempteriana*
9. Lip apical margin not lacerate or erose 10
10. Lip as broad as long, apex shallowly emarginate *V. kaniensis*
10. Lip longer than broad, apex more or less rounded *V. wariensis*
11. Stem quadrate or terete in cross-section; flower not concolorous 12
11. Stem sulcate; flowers greenish, white, cream, or tanned, usually concolorous 16
12. Stems angular in cross-section *V. giullianetii*
12. Stems terete 13
13. Midlobe of the lip long haired *V. ovalis*
13. Midlobe of the lip papillose to short-haired 14
14. Column pubescent on inner surface; lip disc papillate at base *V. platyphylla*
14. Column glabrous; lip disc glabrous at base 15
15. Lip mid-lobe slightly emarginate; callus on mid-lobe oblong, densely papillose *V. sumatrana*
15. Lip mid-lobe subacute; mid-lobe sparsely papillose all over *V. seranica*
16. Inflorescence very dense, many-flowered, usually more than 30-flowered, tepals greenish, flowers small; lip less than 3 cm long *V. havilandii*
16. Inflorescence not very dense, with more than 15 flowers; tepals greenish, white-cream to tanned; flowers larger; lip more than 3.5 cm long 17
17. Tepals tan-colored; lip buff-colored; species from Sri Lanka *V. moonii*
17. Tepals greenish, cream or white; species from Andaman Islands to Indonesia 18
18. Tepals greenish, the lip white *V. albida*
18. Tepals whitish-cream, the apices sometimes greenish, the lip white 19
19. Apical trichomes conspicuous, c. 4 mm long *V. montana*
19. Apical trichomes short, less than 3 mm long 20
20. Callus large with fimbriate, very divided scales almost to their base; species from the Andaman Islands *V. andamanica*
20. Callus small, with lacerate scales; species from Indochina *V. yersiniana*

KEY VII

1. Ovary calyculate, penicillate callus absent, leaves shorter than the internodes of the stem 2
1. Ovary obscurely or not calyculate, penicillate callus well-defined, leaves usually longer than the internodes... 4
2. Flowers tan-colored, the lip white and pink; flowers out-crossing, with slender, basally recurved pods *V. bicolor*

2. Flowers concolorous, yellow, self-pollinated, with thick, strongly recurved about the middle, banana-like pods; plants from savannas, usually on palms 3
3. Lip less than 4.5 cm long; species from Cuba *V. savannarum*
3. Lip more than 5 cm long; species from South America *V. palmarum*
4. Lip strongly undulate-crispate, inflated-vernucose 5
4. Lip not strongly undulate-crispate, not conspicuously inflated nor vernucose 7
5. Inflorescences few-flowered, about 5-flowered; lip glabrous above callus 6
5. Inflorescences multiflorous, more than 10-flowered; lip covered with long trichomes *V. espondeae*
6. Flowers large; lip more than 8 cm long *V. trigonocarpa*
6. Flowers small, lip less than 6 cm long *V. sprucei*
7. Flowers with white to greenish tepals, the lip usually white to greenish, the throat usually lined, the lip may be suffused with yellow, orange or brown on a white-green basal color, distal part of the lip often with papillae or retrorse trichomes, if smooth the flowers not conspicuously yellow 8
7. Flowers greenish-yellow, cream-yellow to yellow with the lip bright yellow to orange, without lines on the lip throat, distal half of the lip lacking papillae or trichomes apart from the penicillate callus 22
8. Leaves narrowly lanceolate to ensiform; lip distal part somewhat warty, with the margins erose, denticulate or fimbriate 9
8. Leaves ovate-lanceolate, oblong to elliptic, not narrowly lanceolate to ensiform, distal part of the lip smooth, warty or papillose, the margins rarely erose-fimbriate 10
9. Flowers small; lip 25-30 mm long; species from the Guyanas *V. fimbriata*
9. Flowers large; lip 35-45 mm long; species widespread in the *V. odorata*
10. Distal part of the lip smooth, except for the penicillate callus, occasionally the axial keels of the lip slightly prominent 11
10. Lip with warts, small papillae or conspicuous, retrorse trichomes on distal part 13
11. Flowers small, white to greenish-white; lip less than 35 mm long; leaves short, up to 4 × 2 cm, much shorter than the internodes; stems less than 5 mm thick *V. hartii*
11. Flowers large, greenish cream; lip more than 60 mm long; leaves medium-size, more than 8 × 3 cm, slightly shorter than the internodes; stems stout, more than 7 mm thick 12
12. Midlobe of the lip defined, lip about 65 × 30 mm when flattened; species from Brazil *V. bahiana*
12. Midlobe of the lip obscure, lip more than 80 × 40 mm when flattened; species from the Caribbean Basin *V. phaeantha*
13. Lip bearing warts, papillae and conspicuous retrorse trichomes on the distal half 14
13. Lip without conspicuous retrorse trichomes on the distal part 20
14. Lip subentire, distal half of the lip completely covered by trichomes *V. ribeiroi*
14. Lip trilobed 15
15. Lip mid-lobe linear, recurved; leaves spatulate-oblongate, mucronate *V. appendiculata*
15. Lip mid-lobe not linear, leaves not spatulate-oblongate 16
16. Trichomes confined to the axial zone of the distal half of the lip 17
16. Trichomes covering all the surface of the distal half of the lip, although they may be longer axially 19
17. Trichomes from the penicillate callus to near the base of the midlobe *V. dungsi*
17. Trichomes from the penicillate callus to almost the lip apex 18
18. Leaves 6 times as long as broad, tapering at base into an obscure petiole; lip midlobe much longer than the side lobes, acute *V. dubia*
18. Leaves about 3.5 times as long as broad, abruptly constricted at the base into a distinct petiole; lip oblong-ovate, mid-lobe emarginated *V. cristagallii*

19. Flowers very large; lip more than 8 cm long; stem conspicuously grooved and minutely papillose; leaves oblong *V. insignis*
19. Flowers not very large; lip less than 6 cm long; stem terete, smooth; leaves elliptic *V. helleri*
20. Leaves elliptic; species from Brazil *V. schwackeana*
20. Leaves oblong-elliptic; species from Central America (but escaped in all tropical areas) 21
21. Leaves oblong, about four times as long as broad *V. planifolia*
21. Leaves lanceolate, about six times as long as broad *V. tahitiensis*
22. Stems more than 8 mm thick; leaves succulent; basal bracts of the inflorescence not conspicuously distichous; lip with a thickened axial cushion near the lip apex, the veins of the distal part of the lip not thickened 23
22. Stems less than 8 mm thick, leaves coriaceous, not conspicuously succulent, basal bracts of the inflorescence conspicuously distichous, lip without a thickened axial cushion near the lip apex, the veins of the distal part of the lip thickened 28
23. Lip conspicuously longer than the petals, the midlobe of the lip strongly emarginated 24
23. Lip about as long as the tepals, the midlobe rounded to slightly notched 25
24. Tepals flared, ovary rather calyculate; species from Central America and NW South America *V. calyculata*
24. Tepals not flared, rather concave, species from SE South America *V. chamissonis*
25. Leaves very large, usually more than 22 × 11 cm, widely elliptic 26
25. Leaves medium-sized, less than 16 × 7 cm, oblong to oblong elliptic 27
26. Midlobe of the lip well-defined *V. pompona*
26. Midlobe of the lip obscure *V. grandiflora*
27. Lip strongly concave *V. pseudopompona*
27. Lip gently concave *V. columbiana*
28. Lip entire; sepals not conspicuously papillose, the papillae, if present, scattered 29
28. Lip obscurely 3-lobed; ovary, sepals and dorsal keel of the petals conspicuously granulose in the outer surface 30
29. Lip acute to subacute; leaves oblong, not acuminate *V. gardneri*
29. Lip apex widely rounded; leaves oblanceolate, acuminate-cuspidate *V. dressleri*
30. Inflorescence many-flowered, up to 60-flowered; leaves up to 26 × 8 cm; lip mid-lobe broadly ovate, with c. 10 thickened keels in the lip apex extending to the lateral lobes; species from Amazonia and Guyanas.....*V. hostmanii*
30. Inflorescence with less than 15 flowers; leaves less than 18 × 7 cm 31
31. Mid-lobe of the lip subquadrate-ovate, with 5-6 thickened keels on the apical, central part of the lip, not extending to the lateral lobes, axial keel low; sepals rounded, slightly subcalyprate; species from Central America.....*V. cribbiana*
31. Mid-lobe of the lip ovate, with c. 8 thickened keels, rather warty on the apical part of the lip, extending to the lateral lobes, 1-3 elevated, axial keels; sepals acute and conspicuously calyprate; species from Peru and Bolivia *V. weberbaueriana*

SYNOPSIS OF *VANILLA*

Listed species, recognized as valid appear in bold face. Those described in *Vanilla* and considered to be synonyms are italicised.

Vanilla Plum. ex Mill., Gard. Dict. abridged de. 4, 3: without page number (1754). Lectotype: *Epidendrum vanilla* L. = *Vanilla mexicana* Mill. (Mansf. in Kulturpfl. 2: 587, 1959)

Myrobroma Salisb., Parad. Lond. t. 82 (1807).

Vanillophorum Neck., Elem. Bot. 3: 184 (1790), nom. inval.

1. ***V. abundiflora*** J.J. Sm. in Bull. Jard. Bot. Buitenzorg ser. 3, 2: 21 (1920). Types: Borneo, Koetei, Soengei Djongkang, Tengaroeng, March 1918, *W.C. van Gelder* 1; Soengei Landak, *J.E. Teysmann s.n.*; Kapoeas, *J.E. Teysmann 109898* (all syn. BO).

DISTRIBUTION: Borneo (Kalimantan Timur, Sarawak).

Similar to *V. kinabaluensis* because of its long inflorescences with more than 100 successive flowers and large leaves, but *V. abundiflora* has smaller flowers, and the apical hairs of the lip are less conspicuous.

It has branched trichomes on the column below the stigma. *Carr 3417* was misidentified as *V. sumatrana*, a plant apparently related to *V. griffithii*.

COLLECTIONS. SARAWAK: *Yii Puan Ching S.61441* (K!); SABAH: Koug, *Carr 3417* (K!).

SOURCES: Smith, J.J. 1920. Bull. Jard. Bot. Buiten. 2: t. 6; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 213-214, fig. 99.

2. *V. acuminata* Rolfe in J. Linn. Soc. Bot. 32: 456 (1896). Type: Gabón, Munda Prov., *Soyaux 134* (holo. K!).

DISTRIBUTION: Gabon, Congo.

This species is very close to *V. africana* and stout plants of it are indistinguishable. The lip is said to have an oblong, obtuse, apiculate mid-lobe, and the disc bears a smaller callus with only about three scales. The lip is missing in the type specimen.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 201, fig. 94.

V. acuta Rolfe = *V. guianensis*

V. acutifolia Lodd. ex W.Baxt. in Suppl. Hort. Brit. 3: 655 (1850). *nomen* (Venezuela)

3. *V. africana* Lindl. in J. Linn. Soc. Bot. 6: 137 (1862). Types: Upper Guinea, Brass R., *Barter 47* (syn. K-LINDL! isosyn. K!); Hort. *Loddiges* (K-LINDL! watercolor only).

DISTRIBUTION: Guinea, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Gabon.

Among the African complex, *V. africana* is characterized by its oblong-lanceolate, long acuminate leaves, the triangular, broadly rounded side lobes of lip, and the ovate midlobe. It is not always easy to distinguish from poorly flowered localities specimens of *V. ramosa*.

COLLECTIONS: EQUATORIAL GUINEA: *Mann s.n.* (K!); *W.W. Sanford 6032* (K!); *Whyte* (K!). GABON: *Griffon de Bellay 501125* (W!); *van der Burg 6691* (K!). CAMEROUN: *Braun s.n.* (K!). NIGERIA: *Richards 3251* (BM!); Hort. *Rotterdam Bot. Gard.* (K!). GHANA: *Johnson 798* (K!); *Johnson 859* (K!); *Bowling 36605* (K!). IVORY COAST: *Hepper & Maley 8196* (K!); *Pérez-Vera 561* (K!). LIBERIA: *Adam 20267* (K!). WITHOUT LOCALITY: Hort *Schiller* (W!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 203-206, fig. 95 (apparently mixed with *V. ramosa*); Summerhayes, V.S. 1968. Flora of West Tropical Africa 3(1): Orchidaceae: 205; Szlachetko, D.L. & Olszewski, S. 1999. Fl. de Cameroun: 284, pl. 100, A-F.

4. *V. albida* Blume, Catalogus 100 (1823). Type: Java, Gunong Salak, Parang, Burungrang, *Blume s.n.* (holo. L).

DISTRIBUTION: Indonesia (Java and Sumatra).

We interpret this species as the plant illustrated by Comber (1990) in *Orchids of Java*. It has flowers with green tepals and a large, deflexed, white lip with conspicuous trichomes at the lip apex. *Vanilla albida* is similar to *V. montana* and *V. yersiniana*, and they have been submerged in the synonymy of the former by some authors. However, *V. montana* has larger trichomes at the lip apex, broader leaves, and *V. yersiniana* has shorter trichomes and whiter tepals, longer sepals and shorter lip. The plant illustrated by Comber (1990) was collected on Gunong Hambali, Lenkong, SW Java, not far from Blume's original locality. Comber (pers. comm.) indicated that the sepals become yellower with age. Blume's plate 67 shows a flower also with greenish tepals, similar to Comber's plant rather than to the Thailand plants identified as *V. albida* in recent years that must be treated as *V. yersiniana*.

COLLECTIONS: INDONESIA, JAVA: *Blume's Rumphia t.67!*; *Zollinger 961* (W!); *C. Doran* (K!); cult. Bogor *s.n.* (K! W!); *Horsfield* (BM!); *Curtis 2271* (BM!).

SOURCES: Blume, C. 1825. Bijdr. 422; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 208-209, fig. 97.

V. anaromatica Griseb. = *V. mexicana*

5. *V. andamanica* Rolfe in Bull. Misc. Inform. Kew 1918: 237 (1918). Type: Andaman Islands, Betapur Valley, 25 Feb. 1916, *C.E. Parkinson 1139* (holo. K!).

DISTRIBUTION: India: Andaman Islands only.

Often relegated to the synonymy of *V. albida* to which is closely related. However, it has a larger penicillate callus in which the scales are so divided, that they look more like hairs than scales. This, together with its isolated distribution in Andaman Islands, suggest that it is better considered as a distinct species.

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 220.

V. angustifolia Willd., Sp. Pl. 4: 121. (1805).

6. *V. angustipetala* Schltr. in Anex. Mem. Inst. Butantan Secc. Bot. 1(4): 19 (1922). Type: Brazil, Sao Paulo, near Morro das Pedras, Iguapé, Dec. 1916, A.C. Brade 7775 (holo. RJ; iso. AMES 114509! K!, R!).

V. rojasiana Hoehne in Arq. Bot. Estado Sao Paulo n.s. 1: 61. t. 82 (1941). Type: Paraguay, Estancia Princeza, Caguazu, , cult. Asunción, April-May 1927, T. Rojas 5082 & 5082-A (syn. RJ; isosyn. AMES 58883! sterile).

DISTRIBUTION: S Brazil, Paraguay and Argentina.

We have examined the type of *V. angustipetala* and it matches well the published drawings of *V. rojasiana*. This species seems to be close to *V. parvifolia*, based on Rodrigues's original plate, which has broader, shorter petals, a more definitively 3-lobed lip, and it lacks the papillae on the disc of the lip, and to *V. verrucosa*, and perhaps not specifically different from them.

COLLECTION: PARAGUAY: *E. Hassler 1294* (K!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 174-176, fig. 84.

7. *V. annamica* Gagnep. in Bull. Mus. Natl. Hist. Nat. sér. 2, 3: 686 (1931). Types: Vietnam, Annam, col de Mangiang, Qui-nhon Prov., *Poilane 17973* (syn. P; isosyn K!); Lang-bian, between B'dle and Dankia, *Poilane 18635* (syn. P; isosyn. AMES 65778!); Lang-bian, *Jacquet 622* (syn. P); Bihn-thuan Prov., *Djiring, Mangnein 82* (syn. P).

DISTRIBUTION: S China and Vietnam.

This species was described from immature buds. However, the branched, cymose inflorescence, with two opposite flowers per cyme, and the large leaves are characteristic. Flowers structure of modern Vietnamese specimens are similar to those of *V. somai*, from Taiwan, with many flat papillae at the lip apex.

COLLECTIONS: CHINA: Guizhou, *Tzi, Luo, Cribb & McGough ASBK 37* (K! PE!); Yunnan, *Cavalerie 3427* (K!).

SOURCES: Gagnepain, F. & A. Guillaumin, A. 1932. Flore Générale de L'Indo-Chine 2. Orchidacées: 584-585, fig. 56; Portères, R. 1954. Le Genre *Vanilla*

et ses Espèces: 179-180, fig. 86; Averyanov, L. 1988. Predvaritelnyy spisok orkhidnykh: 110, fig. 6; Averyanov, L.V. 1994. Identification Guide to Vietnamese Orchids: 76.

V. anomala Ames & L.O. Williams = *Pseudovanilla anomala*

8. *V. aphylla* Blume, Bijdr. Fl. Ned. Ind. 8: 422 (1825). Type: Java, near Sadjvam Province, Bantam; Nusa Kambangan islands, Nov.-March, *Blume 1719* (holo. L)

Limodorum aphyllum Roxb., Pl. Coromandel 1: 34, pl. 41 (1795).

Vanilla parishii Rchb. f., Otia Bot. Hamburg 1: 39 (1866). Type: Myanmar, Tanasserim, *Parish 286* (holo. K!).

DISTRIBUTION: Myanmar, Laos, Thailand, Vietnam, Malaysia, Indonesia (Java).

This is the commonest leafless *Vanilla* of SE Asia. The lip of the specimen of *V. parishii* at Kew bears scattered hairs on the side lobes of the lip, and it is not clear if this represents a distinct character or if, as proposed by Seidenfaden, they are pieces of veins that have broken due to much boiling. *Vanilla aphylla* is closely related to *V. calopogon* of Philippines and *V. wightii* of India.

COLLECTIONS: THAILAND: *Kerr s.n.* (K!); *Kerr 0791* (K!); *Haniff & Nur 4391* (K!); *Put 1907* (K!). VIETNAM: *Pierre 6565* (K!). INDONESIA: Java, *Zollinger 599* (G7888/100! 101! K-LINDL!)

SOURCES: Ridley, H.N. 1924. The Flora of the Malay Peninsula: 201; Gagnepain, F. & A. Guillaumin. 1932. Flore Générale de L'Indo-Chine 2. Orchidacées: 582; Averyanov, L. 1988. Predvaritelnyy spisok orkhidnykh: 110, 112; Seidenfaden, G. & T. Smitinand 1959. The Orchids of Thailand: a preliminary list, part 1: 57, fig. 39; Seidenfaden, G. 1978. Orchid Genera in Thailand VI. Dansk Bot. Arkiv. 32(2): 142, 145-146, fig. 90; Averyanov, L.V. 1994. Identification Guide to Vietnamese Orchids: 77; Holttum, R.E. 1964. Flora of Malaya. Orchids: 98; Comber, J.B. 1990. Orchids of Java: 75.

V. aphylla Wight = *V. wightii*

V. aphylla Eggers = *V. poiteai*

9. *V. appendiculata* Rolfe in Bull. Misc. Inform. Kew 1895: 178 (1895). Type: Guyana (British Guiana),

Corentyne River, *im Thurn s.n.* (holo. K!).

V. purusara Barb. Rodr. ex Hoehne, Arq. Bot. Estado: Sao Paulo; n.s. 1: 127. t. 140 (1944). Syntypes: Brazil, Amazonas, Bom-Lugar, Rio Purús, May 1904, *Huber s.n.* (MG 4721!); Pará, Igapó edge of the Pirapitinga, tributary of the Jutaí de Almeirim, 19 April 1923, *Ducke s.n.* (RJ 18704!).

V. marowynensis Pulle, Enum. Vasc. Pl. Surinam: 118, pl. 4 (1906). Type: Surinam, Upper Marowyne River, near Poeloegoedoe, July, *Versteeg 623* (not seen).

DISTRIBUTION: Guyana, Surinam, Brazil and Peru.

V. appendiculata is distinguished by its large, spatulate, abruptly mucronate leaves, and large flowers with a narrow apical lobe to the lip, that is strongly reflexed and papillose-barbellate. *Vanilla marowynensis* seems to be conspecific, although the illustration, based on an immature bud is inadequate. This species seems to be common in Amazonia.

COLLECTIONS: BRAZIL, Amazonas: *Cavalcante 659* (MG!); PERU, Loreto, *Ruiz & Murphy 255* (K!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 223 and 228, fig. 103 (as *V. marowynensis*).

V. argentina Hicken = *V. chamissonis*

V. aromatica Willd. = *V. planifolia*

V. aromatica Sw. = *V. mexicana*

V. articulata Northr. = *V. barbellata*

10. *V. bahiana* Hoehne in Arq. Bot. Estado: Sao Paulo; n.s. 2, 5: 108, t. 43 (1950). Type: Brazil, Zona litorânea da Bahia, Nov. 1947, *Ferreira Da Cunha s.n.* (holo. SP 54661).

DISTRIBUTION: Known only from Brazil.

A xerophytic inhabitant of the coastal caatinga (or restinga), often with big flowers superficially resembling those of *V. pompona*, with the midlobe of the lip very short. Its closest relative seems to be *V. phaeantha*. Like *V. phaeantha*, the leaves are usually much shorter than the internodes. Some specimens listed as syntypes of *V. gardneri* actually belong to *V. bahiana*.

COLLECTIONS: BRAZIL: BAHIA: *Harley 17366 et al.* (K!); *de Queiroz, Mayo & Nadruz 2918* (K!).

V. bakeri Schltr. = See *V. barbellata*.

V. bampsiana Geerinck = *V. planifolia*

11. *V. barbellata* Rchb. f. in Flora 48: 274 (1865). Type: Cuba, *C. Wright 3352* (holo. W; iso. AMES 70985! K! US!).

V. articulata Northrop in Mem. Torrey Bot. Club: 12(1): 31, pl. 3 (1902). Types: Bahamas, New Providence, Feb., fl. July; London Creek, May; Deep Creek, June, *Northrop 545* (syn. NY according to Correll, 1946).

V. bakeri Schltr. in Repert. Sp. Nov. Regni Veg. 8: 561 (1910). Type: Cuba, Cojimar, Havana Prov., June 1905, *F.C. Baker 5127* (holo. B†); same locality and date, *Baker 5127* (lectotype here designated HAC!).

DISTRIBUTION: Florida, Bahamas, Cuba, Dominican Republic, Puerto Rico, Virgin Islands.

Vanilla barbellata is one of the commonest species in the Caribbean Islands and Florida. It is distinguished by its relatively small flowers and conspicuously 3-lobed, truncate lip.

The holotype of *V. bakeri* was destroyed at B; the only duplicate of it is housed at HAC, but it has only fruits. The original description of the flower suggests that it may have been based in an immature bud of *V. barbellata*, but details of the lip ornamentation do not coincide with the morphology of that species. The lectotype, although sterile, corresponds with the morphology of *V. barbellata*, the fruits being smaller than those of *V. dilloniana*. Its flowering season also corresponds to that of *V. barbellata* and there is also an additional collection of *V. barbellata* from the same locality (*León 6278* HAC!).

COLLECTIONS: *Wright 3337* (BM!). CUBA: *L.B. Smith et al. 3041* (AMES!); cf. *N.L. Britton, F.S. Earle & P. Wilson 4592* (AMES!). BAHAMAS: *N.L. Britton & L.J.K. Brace 540* (K!); *D. Morris s.n.* (K!); *N.H. Nickerson, D. Sammons & B. Kessler 2755* (AMES!); *N.H. & W.L. Nickerson 2826* (AMES!); *L. Zemaitis & N.H. Nickerson s.n.* (AMES!). DOMINICAN REPUBLIC: *A. Liogier 11610* (AMES!) & *15640* (AMES!). WITHOUT LOCALITY: cf. *Pavón* (actually *Sessé and Mociño*) 20-1 (G7889/179!); *Mociño 112* (watercolor!).

SOURCES: Britton, N.L. & C.F. Millspaugh; 1962. The

Bahama Flora: 84 (as *V. articulata*); Acuña, G.J. 1939. Catálogo Descriptivo de las Orquídeas Cubanas: 21-22 (as *V. articulata*); León, F.S.C. & F.S.C. Alain, 1946. Flora de Cuba 1: 351 (as *V. articulata*); Hawkes, A.D. 1948. Notes on *Vanilla barbellata*. Amer. Orchid Soc. Bull. 17(11): 652-653; Correll, D.S. 1946. The American species of "leafless" Vanillas. Amer. Orchid Soc. 15(7): 328-332. Luer, C. 1972. Native Orchids of Florida: 76, pl. 20; Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 171-174, fig. 94.

V. barrereana Veyret & Szlach. = *V. hostmanii*

V. beauchenei A. Chev., Etudes Fl. Afr. Centr. Franc. 1.297 (1913), *nomen*.

12. *V. bertonensis* Bertoni in An. Ci. Parag. ser. I, 8: 10 (1910). Type: Paraguay, Puerto Bertoni, *Bertoni 6039* (holo. not located).

DISTRIBUTION: Paraguay.

A scarcely known plant, described as larger than *V. perexilis* (= *V. parvifolia*), with contorted sepals and a lip with a triangular acuminate midlobe. However, the ovary was described as calyculate, a trait unknown in other members of this group. We suspect that this may be the earliest name for the plant currently known as *V. edwallii*.

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 262-264.

13. *V. bicolor* Lindl. in Edward's Bot. Reg. 24: Misc. 58 (1838). Type: Guyana (British Guiana), *Schomburgk s.n.* (K-LINDL, not traced); lectotype (designated by Christenson, 1995) Guyana, Demerara, watercolor illn. by *Schomburgk s.n.* ex Hort. Loddiges (K-LINDL!).

V. claviculata sensu Lindl. in Ann. and Mag. Hist., ser. 3, 1: 334 (1858), non Sw.

V. wrightii Rchb. f., Flora 48: 273 (1865). Type: E Cuba, 1856-7, *Wright 672* (holo. W! iso. AMES 70991! & 70986! (the last apparently with a flower of *V. cf. barbellata*) BM! G7889/135! K! MO! P!).

V. gratioiosa Griseb., Cat. Pl. Cub. 267 (1866). Type: Based on same type as *V. wrightii* Rchb.f.

V. palmarum sensu Grisebach, Cat. Pl. Cub. 267 (1866), *non* (Salzmann ex Lindl.) Lindl.

DISTRIBUTION: Cuba, Jamaica, Hispaniola, Venezuela, Guyana, Surinam, French Guyana, Trinidad, and Brazil.

A very distinct Caribbean and Guyanan species. The slender plants with small, elliptic leaves, which are much shorter than the internodes, elongate inflorescences, a calyculate ovary, basally recurved pods, tan-colored tepals, a cream-yellowish lip with scattered hairs on the disc, and a poorly penicillate callus are characteristic among American vanillas. It differs from other *Vanilla* species, in that several populations are found in mountain habitats up to 1700 m elevation. Molecular data suggest that it is the sister species of all the American penicillate vanillas.

This species is widely known as *V. wrightii*, a synonym; however, its identity was first elucidated by Sarah Thomas, from Kew and Eric Christenson published a well illustrated paper on the correct identity of this species.

COLLECTIONS: VENEZUELA: *J.A. Steyermark, G.C.K. & E. Dunsterville 92177* (AMES!); *B. Maguire 32967* (AMES!); *B. Maguire & L. Politi 28258* (AMES!). BRAZIL: Roraima: *J.B.F. da Silva 263* (MG!); Amazonas: *B.G.S. Ribeiro 1028* (MG!); ?col. 7885 (BM!). GUYANA: *G.S. Jenman 803 & 4561* (K!); *E.F. im Thurn 43* (K!); *B. Maguire & D.B. Fanshawe 23176* (K!); *N.Y. Sandwith 1331* (K!); *S.S. & C.L. Tillet, R. Boyan 44880* (K!). SURINAM: *Hostmann s.n.* (K!); *B. Maguire 24258* (K!). JAMAICA: *H. Wood* (BM! drawing); [*?Langley*] 7885 (BM!). DOMINICAN REPUBLIC: *B. A.H. Liogier 11474 & 11742* (AMES!); *W.L. Talbot 2363* (AMES!). HAITI: *E.L. Ekman 4355* (AMES! K!). CUBA: *Eggers 5248* (K!); *J.A. Schafer 3218 & 4047* (AMES!); *B. Clemente 1956 & 6626* (AMES!); *B. Alain 373* (AMES!); *C.V. Morton & J. Acuña 3527* (AMES!); *F. León, F. Clement, F. M. Roca 9992* (AMES!); *B. León 15646* (AMES!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 222 and 259-260 (as *V. wrightii*); Christenson, E.A. 1995. The long-lost *Vanilla bicolor*. Amer. Orch. Soc. Bull.: 64(8): 844-847; Schultes, R.E. 1960. Native Orchids of Trinidad and Tobago: 44 (as *V. wrightii*); Foldats, E. 1969. Flora de Venezuela. Orchidaceae 1: 127-129 (as *V. wrightii*); Gloudon, A. & C. Tobisch. 1995. Orchids of Jamaica: 209 (as *V. wrightii*); Acuña, G.J. 1939. Catálogo Descriptivo de

las Orquídeas Cubanas: 22-23 (as *V. wrightii*); León, F.S.C. & F.S.C. Alain. 1946. Flora de Cuba I: 352 (as *V. wrightii*); Martius, F.P., Fl. Brasiliensis 3: t. 4: 149. 1896.

14. *V. borneensis* Rolfe in J. Linn. Soc. Bot. 32. 460 (1896). Type: Kalimantan, Banjarmasin, *Motley 1248* (holo. K!).

V. pilifera Holttum in Gard. Bull. Singapore 13: 251-253 (1951). Type: Malaysia: Kota Tinggi, Johore, *le Doux s.n.* (holo. SING).

DISTRIBUTION: Reported from NE India, Thailand, Malaysia and Indonesia (Kalimantan).

This species was described from a fruiting specimen, and its flowers are unknown. No additional specimens are known from southern Kalimantan, where the species was originally collected. The elliptic-oblong, long acuminate leaves are different from other Bornean vanillas, such as *V. griffithii*. The few-flowered racemes separate it from the densely flowered racemes of *V. havilandii* (or the Javanese *V. albida*), or the long, many-flowered racemes of *V. abundiflora* and *V. kinabaluensis*. However, it looks very similar to specimens of *V. pilifera* collected in Sabah, northern Borneo, especially in leaf shape and the few-flowered, rather zigzag rachis of the inflorescence. Thai specimens of *V. pilifera* have much narrower, lanceolate, acute leaves, and shorter inflorescences. *V. montana*, from peninsular Malaysia, has oblanceolate, abruptly acuminate leaves that are also similar.

It is easily distinguished by its lanceolate to elliptic, often narrow, short leaves and conspicuously hirsute disc of lip. It is closely related to *V. diabolica*, from Sulawesi.

A Burbidge specimen (*Burbidge s.n.*, BM) from Sabah, NW Borneo (Tawaran and Tampasuk rivers), may belong to *V. kinabaluensis*, rather than to *V. borneensis*, as suggested by Rolfe.

COLLECTIONS: THAILAND: *Put 2285* (BK C K!). MALAYSIA: SABAH: *A. Lamb 87/83* (K! specimen and drawing); *Daim Andau 440* (K! sterile); *SAN 122464* (K! sterile); *SAN 68739* (K! sterile); *A. Talip 54914* (K! sterile); *J. Beaman 7804* (K! sterile); *L. Madani SAN 89511* (K! sterile).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 215-216; Portères, R. 1954. Le Genre *Vanilla*

et ses Espèces: 169-170 (as *V. pilifera*); Teo, C.K.H. 1985. Native Orchids of Peninsular Malaysia: 108-109 (photo. of *V. aphylla*?; as *V. pilifera*); Seidenfaden, G. & T. Smitinand 1959. The Orchids of Thailand: a preliminary list, part 1: 57, fig. 39 (in part; the illustration based on TS 4075, may be *V. yersiniana*?; as *V. pilifera*); Seidenfaden, G. 1978. Orchid Genera in Thailand VI. Dansk Bot. Arkiv. 32(2): 142-143, fig. 88 (as *V. pilifera*); Seidenfaden G. & J.J. Wood. 1992. Orchids of Peninsular Malaysia and Singapore 125 (as *V. pilifera*). Holttum, R.E. 1964. Flora of Malaya. Orchids: 95-96, fig. 16A (as *V. pilifera*).

15. *V. bradei* Schltr. ex Mansf in Repert. Sp. Nov. Regni Veg. 24: 243 (1928). Type: Brazil, Sao Paulo, *A.C. Brade 7573* (holo. B†, AMES drawing!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 258-259.

16. *V. calopogon* Rchb. f., Otia Bot. Hamburg. 1: 40 (1878). Type: Philippines, Luzón, *Cuming 2070*, 1841 (holo. W!; iso. BM! G7889/99 168! K-LINDL! K!).

DISTRIBUTION: The Philippines (Luzón).

This species is very closely related to *V. aphylla* and *V. wightiana*. However, it has slightly larger flowers and is endemic to Luzón.

COLLECTIONS: LUZON: *Loher 630* (K!).

SOURCE: Valmayor, H.L. 1984. Orchidiana Philippiniana 1: 322.

17. *V. calyculata* Schltr. in Repert. Sp. Nov. Regni Veg. 7: 42 (1920). Type: Colombia, *M. Madero s.n.* (holo. B†).

DISTRIBUTION: Honduras, El Salvador and Colombia.

The status of *V. calyculata* remains uncertain and no original material has been located. However, the description suggests that the name must be applied to the specimens listed below. Its calyculate ovary, long emarginate midlobe of the lip, small leaves and the relatively high elevation of its habitat are characteristic. This species is closely related to *V. chamissonis* from Brazil. Specimens from El Salvador have been misidentified as *V. phaeantha* (Hamer, 1974).

COLLECTIONS: EL SALVADOR: *Pank in Hamer 203* (AMES!). HONDURAS: Comayagua, *Yuncker et al. 6045* (AMES! G78889/152! K!). COLOMBIA:

Valle, *Dryander* 2379 (BM!); Tolima, *Lehmann* 2263 (BM! G7889/175!); *Lehmann* 8378 (K! watercolor); La Plata, cf. *Lehmann* 6278 (AMES!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 247. Hamer, F. 1974. Las Orquídeas de El Salvador 2: 375, t. 41 (as *V. phaeantha*)

V. carinata Rolfe = see in excluded species

18. *V. chalogii* Finet in Bull. Soc. Bot. France; 56: 102 (1909). Type: Gabon, near Libreville, *Chalot* 4027 (holo. P).

DISTRIBUTION: Endemic to Gabon.

This species has a conspicuous, shallowly saccate lip, with a very reduced, recurved, apical lobe. It is similar to *V. nigerica* and *V. seretii*, in which the stems are verrucose, and the white and pink flowers are much larger.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 170-171, fig. 82; Szlachetko, D.L. & S. Olszewski. 1999. Fl. de Cameroun: 280-282, pl. 100, A-F.

19. *V. chamissonis* Klotzsch in Bot. Zeitung 4: 564 (1846). Type: Brazil, *Chamisso s.n.* (lecto. LE! photo).

DISTRIBUTION: Brazil.

Two different taxa have been called *V. chamissonis* in recent times. The true *V. chamissonis* has a very long midlobe of the lip (e.g. drawings of Portères, 1954, fig. 104; Martius, 1986, t. 32 or Hoehne's illustration of *V. chamissonis* var. *longifolia*); the other one is *V. vellozii*, reduced by most recent authors to a variety of the former. *Vanilla chamissonis* is similar to the *V. calyculata* from Colombia and Central America. *Vanilla vellozii* is different in its shorter segments and subentire lip, and it is not clear if it is a member of the *V. chamissonis* or *V. pompona* complexes.

COLLECTIONS: BRAZIL: *Glaziou* 15661 (K!); The specimen *Glaziou* 14302, "Environs of Rio Janeiro", was assigned by Rolfe (1896) to *V. vellozii*, but, although with very bad preserved flowers, it seems to have the very long lip characteristic of *V. chamissonis*; a similar case occurs with the *Glaziou* specimen from Copacabana (apparently that considered by Rolfe to be his number 11621). GOIAS, cf. *A. Glaziou* 22151 (G 7889/115!). BAHIA: *M. Blanchet s.n.* (G 7889/114!); *Dusén s.n.* (AMES 86539!). Rio de Janeiro, *Miers* (BM!); *L.A. Gattoni s.n.* (AMES 66126! AMES

66339! AMES 66345!).

SOURCES: Martius, F.P., Fl. Brasiliensis 3: pt. 4: 148, t. 32. 1896; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 190, fig. 90 (as ?*V. vellozii*), p. 191-192 (as *V. argentina*); Pabst, G.F.J. 1966. As: Orquídeas do Estado da Guanabara. Orquídea 28(2-6): 169-170.

20. *V. claviculata* (W.Wright) Sw. in Nov. Act. Soc. Sc. Upsal. 6: 66 (1799). Type: Jamaica, *Swartz s.n.* (lecto. BM!, here designated).

Epidendrum claviculatum W. Wright in London Med. J. 8(3): 254 (1787).

DISTRIBUTION: Cuba, Jamaica, Hispaniola, Grand Cayman, Puerto Rico, St. Thomas.

It belongs to the American leafless group but can bear fugaceous, small leaves, up to 8 × 1 cm, which are conspicuously apiculate. The lip is not conspicuously trilobed at apex, as its allies, but rather rounded, and it has a penicillate callus of dense forked hairs and rows of similar hairs towards the apex, but not dense.

COLLECTIONS: CUBA: *León & Alain* 19346 (AMES!); *R.A. Howard* 6522 (AMES!); *A.H. Liogier* 11493 (AMES!); *R.M. Gray s.n.* (AMES! K!). DOMINICAN REPUBLIC: *R.A. & E.S. Howard* 8654 (AMES!). PUERTO RICO: *A.G. Kevorkian s.n.* (AMES!). JAMAICA: *H. Wood* (BM! drawing); *C. Whitefoord* 1423 (BM!). GRAND CAYMAN: *M. Brunt* 2186 (BM!); *W. Kings G.C.* 412 (BM!).

SOURCES: Sloane, H. 1725. Jamaica Nat. Hort. t. 224; Fawcett, W. & A.B. Rendle. 1910. Flora of Jamaica 1. Orchidaceae 16-17, pl. 2: 18-19; Acuña, G.J. 1939. Catálogo Descriptivo de las Orquídeas Cubanas: 23 (as *V. parasitica*); Correll, D.S. 1946. The American species of "leafless" Vanillas. Amer. Orchid Soc. Bull. 15(7): 328-332; León, F.S.C. & F.S.C. Alain. 1946. Flora de Cuba 1: 352, 354; Gloudon, A. & C. Tobisch. 1995. Orchids of Jamaica: 206-207; Castillo Mayda, M. & J.D. Ackerman. 1992. The Orchids of Puerto Rico and the Virgin Islands: 52, pl. 10; Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 174, fig. 95.

V. claviculata sensu Lindl. in Mem. Am. Acad. n.s. 8: 219 (1861) = *V. bicolor*

21. *V. columbiana* Rolfe in J. Linn. Soc. Bot. 32: 468 (1896). Type: Colombia [New Granada], Valley of the Magdalena, February, *Goudot s.n.* (holo. K!).

The type material is very unsatisfactory, making an accurate description of this species problematic. The dissected flower of the type, probably an immature bud, has a very neat midlobe to the lip. We have assigned to this concept specimens from the *V. pompona* complex with small leaves, resembling those of *V. phaeantha*, with flowers with green sepals and petals and a white lip with a yellow edge, but we would like to examine more material from the Magdalena Valley. It is possible that they might better be attributed to the plant we are treating here as *V. calyculata*.

COLLECTIONS: COLOMBIA: *F.A. Barkley & M. Valderama 35275* (AMES!); *H. García-Barriga 15373* (AMES!); *J.L. Zarucchi & C. E. Barbosa 3637* (AMES! MO).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 229-231, fig. 103.

V. correllii Saulea & R.M. Adams = *V. poitaei*

22. *V. costaricensis* Soto Arenas ined.

DISTRIBUTION: Endemic to Costa Rica.

This new species of *Vanilla* is closely related to *V. mexicana*, from the West Indies and NE South America. However, *V. costaricensis* has a very short midlobe to the lip and large bracts similar to those of *V. inodora* Schiede. The species was illustrated by Rafael Lucas Rodríguez (1986), but apart from this record, it is known only from the type and another collection from the same locality. As far as is known, *V. mexicana* is not found in Central America.

SOURCES: Lucas Rodríguez, R., D.E. Morta, M.E. Barahona & N.H. Williams. 1986. Géneros de Orquideas de Costa Rica: 70-71.

23. *V. coursii* H. Perrier in Rev. Int. Bot. Appl. Agric. Trop. 30: 435 (1950). Type: Madagascar, N of Antalaha, *Cours G6* (holo. P!)

DISTRIBUTION: Endemic to Madagascar.

Very poorly known. We have been unable to examine material of this leafy Madagascan species, and from the literature it is difficult to suggest its affinities, the presence of leaves, the hexagonal lip and the very small flowers are different from other species of the island.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 170; DuPuy, D., P. Cribb, J. Bosser & J. & C. Hermans:1999. The Orchids of Madagascar: 207.

24. *V. crenulata* Rolfe in J. Linn. Soc. Bot. 32: 477 (1896). Types: Sierra Leone, Bumban to Lokko, *Scott Elliot 5733* (syn. K!; isosyn. BM!); Ashanti, Prahsu, *Cummins 4* (syn. K!).

DISTRIBUTION: W and WC Tropical Africa.

Another member of the *V. africana* complex, often considered as conspecific with *V. ramosa*. It is characterized by its broad leaves, unbranched inflorescence, and flowers with a broader and less acute crenulate front lobe of the lip. Characteristic is the presence of very broad, oval bracts at the base of the raceme. Summerhayes (1968) also indicated a larger lip, midlobe and column in *V. crenulata*, compared with *V. ramosa*.

In living condition, *V. crenulata* flowers are easily distinguished by their conduplicate, gibbose midlobe of the lip, with a penicillate callus at the top of the gibba. In their relatives (e.g. *V. ramosa*) the lip is rather flat, but this character is difficult to see in herbarium specimens. Szlachetko & Olszewski (1999) considered *V. crenulata* to be a synonym of *V. africana*. COLLECTIONS: GUINEA: *Schnell 3086, 799* (K!). LIBERIA *Bunting s.n.* (BM!); *Barker 1265* (K!); *Jansen 1013* (K!); *Baldwin 10661A, 10966, 11116* (K!); *Whyte s.n.* (K!); *Blickenstaff 92* (K!); *Linder 46, 76* (K!). GHANA: *Fishlock 57* (BM! K!); *Wilson 1036* (K!); *Bowling 38137* (K!); *Westwood 112* (K!); *Irvine 1186, 1808* (K!); *Vigne 3062* (K!); *Darko 1018* (K!); *Morton GC6553* (K!). IVORY COAST: *Pérez-Vera 642* (K!); *de Wilde 576* (K!); *Chevalier B22383* (K!); *Leeuwenberg 3054* (K!). NIGERIA: *Miles s.n.* (BM!). GABON: *Le Testu 1413* (BM!); *van der Laan 834* (K!). SIERRA LEONE: *Deighton 2496, 2963, 6151* (K!); *Dawe 439* (K!); *Bobob s.n.* (K 37879!); *Segeback 1537* (K! also photos); *Thomas 3432* (K!). PRINCIPE: *Exell 623* (BM!). ZAIRE: *Lebrun 3241* (K!). WITHOUT LOCALITY: *Johnson 24* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 196-198, fig. 92; Geerinck, D. 1984. Flore D'Afrique Centrale (Zaire, Rwanda-Burundi): 239-242; Summerhayes, V.S. 1968. Flora of West Tropical Africa 3(1): Orchidaceae: 205-206. Johansson, D. 1974. Acta Phytogeographica Suecica 59: 44-45.

25. *V. cribbiana* Soto Arenas, ined.

DISTRIBUTION: Known from Mexico (Veracruz, Oaxaca, Chiapas), Guatemala, Belize, and Honduras.

Vanilla cribbiana is a member of the *V. hostmanii* group. Its fruits are fragrant, and probably of some interest, but the vine is not a strong grower and does not produce fruits regularly.

COLLECTIONS: BELIZE: *C. Whitefoord* 1816 (BM!). HONDURAS: *O. Ames II-211* (AMES!).

26. *V. cristagallii* Hoehne in Arq. Bot. Estado: Sao Paulo; n.s. 1: 125 (1944). Type: Brazil, Amazonas, Sao Paulo de Olivença, 23 Oct. 1931, *Ducke s.n.* (holo. RJ 14512!).

V. cristato-callosa Hoehne in Arq. Bot. Estado: Sao Paulo; ns.s. 1: 126. t. 137 (1944). Type: Brazil, Amazonas, Manaus, 20 Oct. 1935, *Ducke s.n.* (holo. RJ 37468!).

DISTRIBUTION: Amazonian Brazil.

This species, like several other Amazonian species, has an apical lobe adorned with retrorse trichomes or transverse crests. The difference between the types of *V. cristagalli* and *V. cristato-callosa* is mostly in the size of the flowers and lip, but they seem to represent the same species.

SOURCE: Hoehne, F.C. 1944. Arq. Bot. Estado Sao Paulo, n.s. 1: 125.

27. *V. cucullata* Kraenzl. ex J. Braun & K. Schum., Mitth. Deutsch. Schutzgeb. 2: 161 (1889). Type: Cameroon, *Braun 4* (holo. B†).

V. africana Lindl. subsp. *cucullata* (Kraenzl. ex J. Braun & K. Schum.) Szlach. & Olszewski in Fl. Cameroun 34: 286 (1988).

Perhaps not different from *V. crenulata*. In this species of the *V. africana* complex, the oblong-elliptic lip is acute, and the petals and sepals rather broader.

COLLECTIONS: CAMEROUN: *Zenker 525* (AMES! BM! G 7889/116/117/118! P).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 195-196.

28. *V. decaryana* H. Perrier in Bull. Mus. Hist. Nat. (Paris) 6: 194-195 (1934). Types: Madagascar, Domaine du Sud-Ouest: Morondava, *Greve 39* (syn. P!); Ambovombe, Jan. 1925, *Decary 3531* (syn. P!; isosyn. K!); Behara, E of Ambovombe, 17 Nov. 1931, *Decary 9313* (syn. P!); Mahatomotsy, N of Ambovombe, 9 Dec. 1931, *Decary 9503* (syn. P!).

DISTRIBUTION: SW Madagascar.

A member of the *V. roscheri-V. madagascariensis-V. phalaenopsis* group, but with smaller more numerous flowers, greenish sepals, a column only 14-16 mm long and with narrower rhombic lip with the keels of the disc just to near the border of the lip, more conspicuous and with hairs shorter and not as fleshy.

COLLECTIONS: MADAGASCAR: *O'Connor 98* (K drawing!).

SOURCE: Du Puy, D., P. Cribb, J. Bosser & J. & C. Hermans. 1999. The Orchids of Madagascar: 207.

V. denticulata Pabst = *V. odorata*

29. *V. diabolica* P.O'Byrne in Malayan Orchid Rev. 30: 67-70, figs. (1996). Type: Indonesia, Sulawesi, Tenggara-Buton Island, near Maligano, *O'Byrne SB47V* (holo. SING; drawing at K!).

This species is closely related to *V. borneensis*, but *V. diabolica* has elongated inflorescences, smaller flowers with two raised bodies at the base of the lip, shorter and broader tepals and a lip in which the veins of the throat are orange rather than purple.

30. *V. dilloniana* Correll in Amer. Orch. Soc. Bull. 15(7): 331, f. 1-7 (1946). Type: USA, Florida, Brickell Hammock, Dade County, *Humes s.n.* (holo. AMES).

DISTRIBUTION: Cuba, Florida, Hispaniola, Puerto Rico, and Saint Thomas.

Distinguished by its starry flowers, conspicuously trumpet-shaped 3-lobed lip, edged with rich purple, in which the midlobe is triangular and longer, and with yellowish papillae towards the lip apex. The only known population in Florida has been wiped out, although plants survive in cultivation.

Although similar to the other leafless Caribbean species, it is easily distinguished when flowering material is at hand. *Vanilla clavícula* has an entire lip; from *V. barbellata* it is distinguished by its larger flowers and much longer midlobe of the lip. Many specimens bear small leaves, similar to those found in *V. claviculata* and *V. poitaei*, but rarely seen in *V. barbellata*. *Vanilla poitaei* has a larger lip and the margins are crisped.

COLLECTIONS: CUBA: *Wright s.n.* (K-LINDL!); *Jack 5200* (AMES!); *Wright s.n.* (AMES 70987, in part)! PUERTO RICO: *Pennington s.n.* (AMES 45836!); *Pennington s.n.* (AMES 43655!); *Sintenis 3932* (BM!); *Sintenis 4934* (K! fruits only). DOMINICAN

REPUBLIC: *Fuertes s.n.* (AMES!). ST. THOMAS: *Ostenfeld 235* (G7889/119!).

SOURCES: Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 171, fig. 93. Britton, N.L. and C.F. Millspaugh. 1962. The Bahama Flora: 83 (as *V. eggersii*). McCartney, C. 2000. African affinities. *Orchids*: 69(4): 341 (as *V. dilloniana*).

V. domestica Hort., *nomen* = ?*V. planifolia*

V. dominiana Hort. ex Gentil, *Liste Pl. Cult. Serres Jard. Brux.* 192 (1907), *nomen*.

31. *V. dressleri* Soto Arenas ined.

DISTRIBUTION: Costa Rica, Panama and W Colombia.

This large-flowered species is a member of the *V. hostmanii* group. Among the group, it is distinguished by the rather lax inflorescence, with distant flowers (c. 1 cm apart), patent bracts, subentire lip, with a subrhombic blade, and very scarcely papillose sepals; *V. cribbiana*, *V. hostmanii* and *V. ruiziana* have conspicuously granulose sepals. From *V. cribbiana* it is additionally distinguished by the narrower, thinner leaves which are more long acuminate-cuspidate, laxer inflorescences, less defined apical lobe, veins of the disc more conspicuously thickened, and flowering time mostly in March-May, not in July-August. *Vanilla hostmanii* from Amazonia has very long inflorescences which bear much more flowers (e.g. 40-50) and the leaves are larger, thicker, not as acuminate-cuspidate. *Vanilla ruiziana*, from Peru and Bolivia has larger, broader, less acuminate-cuspidate, and thicker leaves, but is similar to *V. dressleri* in their rather elevated axial keels of the lip. *Vanilla gardneri* from Brazil has a subacute lip apex and oblong leaves, not cuspidate.

COLLECTIONS: PANAMA: *Knapp & Mallet 4621* (MO!); *Williams in SEL 56-76-11* [accession num.], *Pridgeon s.n.* (SEL 019244!); the leaves; flowers may belong to *V. pseudopompona*); *Dressler; Luer; Luer & Taylor 768* (SEL!); COSTA RICA: *Haber 8471 & Cruz* (CR MO!); *Herrera 1840* (CR MO 3864177!); *Liesner 14435* (MO!); *Todzia 1291* (LL!); *Lankester s.n.* (SEL!). COLOMBIA: *Cuatrecasas 16550* (AMES!); *Cuatrecasas 15220* (AMES!); *García C. & Agualimpia 325* (MO!); Choco, *Ingram 1421* (SEL!); *Ingram 1422* (SEL!).

32. *V. dubia* Hoehne in *Arq. Bot. Estado Sao Paulo n.s.* 1: 126 (1944). Type: Brazil, Minas Gerais, Belo Horizonte, *Schwacke 11107* (holo. RJ 37014!).

DISTRIBUTION: Brazil.

Closely related to *V. appendiculata*, *V. cristagallii* and *V. schwackeana*, and with the characteristic papillose apical apex of the lip of many Brazilian species.

V. duckei sensu Hoehne (1945) = *V. planifolia*

33. *V. dungsii* Pabst in *Bradea* 2, 10: 49 (1975). Type: Brazil: Estado do Rio de Janeiro, near Novo Friburgo, 1300 m, Febr. 1973, *Dungs s.n.* (holo. HB 59052!).

DISTRIBUTION: Brazil.

Little is known of this species. It was stated in the original description that it is allied to *V. cristatocallosa* (= *V. cristagallii*). The clump retrorse papillae towards the apex of the lip is certainly characteristic of that group of *Vanilla*.

V. eggersi Rolfe = *V. poitaei*

V. ensifolia Rolfe = *V. odorata*

V. epidendrum Mirb. = ?*V. mexicana*

34. *V. edwalli* Hoehne in *Arq. Bot. Estado Sao Paulo n.s.* 1: 61. t. 81 (1941). Type: Brazil, Sao Paulo, Serra da Cantareira, Jan. 1902, *Gustavo Edwall 6003* (holo. SP).

DISTRIBUTION: Brazil and Argentina.

A species with long acuminate segments and a rather unornamented lip, except by the longitudinal lamellae. It is very probable that *V. edwalii* is a synonym of *V. bertonensis* Bertoni, which original material has not been available to us. From *V. parvifolia* differs by its acuminate midlobe of the lip.

COLLECTIONS: BRAZIL: Distrito Federal: cf. *E.P. Heringer 5001 et al.* (MG!).

35. *V. espondae* Soto Arenas ined.

DISTRIBUTION: Endemic to Colombia.

This is one of the most beautiful *Vanilla* species. It has been found in the rainy, Pacific coast of Colombia and on a tributary of Magdalena River. Although is not closely related to any other *Vanilla* species, it could be related to *V. trigonocarpa*. It is distinguished by the very large papillae covering the lip apex.

V. fasciola Spreng. = *Taeniophyllum fasciola*

36. *V. fimbriata* Rolfe in Bull. Misc. Inform. Kew 1899: 133 (1899). Type: Guyana (British Guiana), Barima River, *Jenman 6771* (holo. K!; iso. K!).

DISTRIBUTION: Brazil and Guyana.

Very close to *V. odorata*, or perhaps conspecific. The type material is not good enough to check the differences with *V. odorata*, but the flower size is smaller (the lip 25-50 mm long whereas it is 35-45 mm in *V. odorata*). This could be a result of the preservation process. However, the leaves are rather shorter and the stems more floriferous than in any other *V. odorata* specimen that we have examined.

COLLECTIONS: PARA: *Plowman et al. 9868* (MG!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 245-247, fig. 111.

V. fragrans Ames = *V. planifolia*

37. *V. francoisii* H. Perrier in Notul. Syst. (Paris) 8: 37 (1939). Type: Madagascar, S Toamasina, Ambilo, cult. *François* (holo. P!).

DISTRIBUTION: Endemic to Madagascar.

A very rare species of which we have seen the type and one other collection. It was described as having slender stems, very small leaves and small, few-flowered racemes; the flowers have a trumpet-shaped lip with reflexed disc. It may well be conspecific with *V. perrieri*.

COLLECTION: MADAGASCAR: between Ampanihy and Andraka, *Capuron 479* (P!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 180-181; Du Puy, D., P. Cribb, J. Bosser & J. & C. Hermans. 1999. The Orchids of Madagascar: 207.

38. *V. gardneri* Rolfe in Bull. Misc. Inform. Kew 1895: 177 (1895). Types: Brazil, Morro do Flamengo, near Rio de Janeiro, *Gardner 245* (lecto., K! **here designated**); Parnagua District, Piahy Prov., *Gardner 2733* (syn. K!); Natividade, Goyaz, *Gardner 3449* (syn. K!); Pernambuco, at Iguarassa, *Ridley, Lea and Ramage s.n.* (syn. K!); *Burchell 894* (syn. K! sterile); near Rio, San José da Laranjeira, *Gardner 9829* (syn. K! sterile).

DISTRIBUTION: Brazil.

The entire, rhombic, subacute to obtuse lip of this species is very characteristic, and similar only to the Central American *V. dressleri*. It has also the thickened

veins in the lip apex and the distichous arrangement of the basal bracts of the inflorescence characteristic of the *V. hostmanii* group. The species seem to be rare and we are basing our concept of this entity upon Hoehne's published drawing and the lectotype, since other materials are fragmentary or inadequate, and characters of the surface of sepals and ovary, typical of the *V. hostmanii* group, have not been examined.

The information on the lectotype, in Rolfe's handwriting, was probably obtained from a Gardner's note in Hooker, London Journal of Botany 1: p. 542; cited in the protologue. The original data are "245. *Vanilla* sp. Scentless. Climbing on the stump of an old Tree. Rio Comprido [?] common in the woods about Rio but seldom seen in flower. I could barely obtain 2 flowers. March 1836."

The syntypes *Ridley, Lea and Ramage s.n., Gardner 2733* and *3449* probably belong to *V. bahiana*, and are not conspecific with *Gardner 245*, selected here as the lectotype. *Burchell 9828* has no flowers and the leaves are very different from the lectotype and it is doubtfully conspecific with it.

COLLECTIONS: BRAZIL: *Glaziou 20709* (BM!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 192; Pabst, G.F.J. 1966. Orquídea 28(2-6): 169-170.

39. *V. giulianettii* F.M. Bailey in Queensland Agric. J. 7: 350 (1900). Type: Papua New Guinea (British New Guinea), 15 Dec. 1909, *Giulianetti 1906* (holo. BRI; iso. K!).

DISTRIBUTION: New Guinea.

This scarcely known species has very large leaves, different from those of the New Guinean *V. ramificans*. However, we have not examined flowering specimens to compare it with the New Guinean vanillas described by Schlechter, which also have large leaves (*V. kaniensis*, *V. kempteriana* and *V. wariensis*).

COLLECTIONS: PAPUA NEW GUINEA: Morobe, *Gillison NGF 25021* (K!); Western Dist., *Ridsdale & Galore NGF 33728* (K!); Northern Dist., *Carr 17133* (BM!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 221.

40. *V. grandiflora* Lindl., Gen. Sp. Orch. Pl. 435 (1840). Type: French Guiana, *Martin s.n.* (holo. K-LINDL!).

V. clavicula Duss, *nomen*.

V. lutescens Moq. ex Dupuis, Rev. Hort. ser. 4, 5: 121, f. 24 (1856).

DISTRIBUTION: Venezuela, Trinidad & Tobago, Guyana, Peru, and Brazil.

Vanilla grandiflora has somewhat larger flowers than *V. pompona* (lateral sepals up to 8.4 cm in the type specimen). The sepals are narrower, subacute, the petals less rounded, and the lip has a subquadrate apex, not deeply notched as *V. pompona*.

COLLECTIONS: GUYANA: *Smith 2474* (G 7889/122! K!); *im Thurm s.n.* (K! K drawing!). VENEZUELA: *Pittier 9460* (G 7889/149!). TRINIDAD & TOBAGO: *Hart 3* (K!); *Broadway 4565* (BM!); *Broadway 41912* (BM!); *Hance 5285* (BM!). PERU: *Klugg 3685* (BM!). BRAZIL: *Rondonia, Rosa et al. 5060* (MG! fruit only); *Rosa et al. 4915* (MG!); *Roraima, Pires et al. 16778* (MG! fruits only).

SOURCES: Schweinfurth, C. 1958. Orchids of Peru I. *Fieldiana: Botany* 30: 43-44 (as *V. pompona*); Schultes, R.E. 1960. Native Orchids of Trinidad and Tobago: 42 (as *V. pompona*); Dunsterville, G.C.K. & L.A. Garay. 1959. Venezuelan Orchids Illustrated 1: 434-435 (as *V. pompona*); Foldats, E. 1969. Flora de Venezuela. *Orchidaceae* 1: 125-127, fig. 43 (as *V. pompona*).

41. *V. grandifolia* Lindl. in J. Linn. Soc. Bot. 6: 138 (1862). Type: Principe (Prince's Island), *Barter 1981* (holo. K! drawing K-LINDL! tracing W!).

DISTRIBUTION: Democratic Republic of the Congo, Gabon, Principe Island.

This species is characterized by its large, broadly elliptic to suborbicular leaves, abruptly apiculate or rather thin substance. Floral morphology suggests a close relationship with *V. imperialis*, with a very large rostellum and a trumpet-shaped, concave lip, which is apiculate at apex (after drawings sent by de Wildeman to Kew). Portères' fig. 85 (1954) shows a straight, undulate, entire lip lacking the characteristic apicule at apex.

COLLECTIONS: PRINCIPE: *Henriquez* (K!); *Monteiro* (K!). Democratic Republic of the Congo: *Louis 2599* (B, K!) & *10800* (K!) *de Wildemann s.n.* (K fragment ex Berlin!). GABON: *Le Testu 6077* (BM! K!), *8445* (BM! K!) & *9308* (BM! K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 176-178, fig. 85; Szlachetko, D.L. & S.

Olszewski. 1999. Fl. de Cameroun: 292, t. 103, G-K.

V. grandifolia var. *lujae* (De Wild.) Geerinck = *V. imperialis*

V. gratiosa Griseb. = *V. bicolor*

42. *V. griffithii* Rchb. f. in Bonplandia (Hanover) 2: 88 (1854). Types: Malacca, *Griffith 281* (lectotype W, here designated); Tabong, Malacca, 1844, *Griffith s.n.* (syn. K-LINDL! probable duplicate at AMES 71377!).

V. tolypephora Ridl. in Trans. Linn. Soc. London, Bot. 3: 276 (1893). Type: Malaysia, Penang and the Island Pulau Ubin, lying in the strait between Singapore and Johore, and in Selangor, *Singapore collector 3924* (holo. BM!).

DISTRIBUTION: Peninsular Malaysia, Singapore, Borneo (Brunei), Sumatra. Expected from S: Thailand.

Vanilla griffithii is a distinct species because the "ball" of hairs instead of the penicillate callus of allied species. The midlobe is itself deeply bilobed. The floral buds are very truncate-rounded. Sterile collections can be identified by the very broad leaves and many capsules on the inflorescences, as if they be self-pollinated.

COLLECTIONS: MALAYSIA: *Griffith s.n.* (K-LINDL!); *Griffith 7401* (K-LINDL!); *Griffith s.n.* (AMES!); *Ridley 1969* (BM!); *Curtis 2271* (K!); *Wray in King 2537* (K!); *King 2996* (K!); *King 7528* (K!); *Maingay 1660* (K!) & *3255* (K!); *Scortechini s.n.* (K!); *Curtis 1179* (K!); *Henderson 20378* (K!); *Ngadiman in Henderson s.n.* (K!); *Ahmad S.324* (K! sterile); *Sidek bin Kiah S.248* (K!); *Whitmore FRI 3706* (K!); *Negri Sembilan, FRI 27529* (K!); *Evans s.n.* (K!); *Tahit 1233* (K!); *Mondi 289* (K! fruits only); *Leopold & Ag. Amin SAN 86237* (K! fruits only); *Collenette 643* (K!); *Scortechini 1080* (K!); *Cheng FRI 27529* (K!); *Perlis, Kaboch 15197* (K!). SINGAPORE: *Lobb 226* (K!); *Curtis* (K!); *Ridley 3924* (BM!). BRUNEI: *Johns 7456* (K!); *Wong 974* (K!); *Boyce 452* (K!).

SOURCES: Ridley, H.N. 1924. The Flora of the Malay Peninsula: 201; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 168-169; Teo, C.K.H. 1985. Native Orchids of Peninsular Malaysia: 107-108. Seidenfaden, G. & T. Smitinand. 1959. The Orchids of Thailand: a preliminary list, part 1: 58; Seidenfaden, G. 1978. Orchid Genera in Thailand VI. *Dansk Bot. Arkiv.* 32(2): 142, 144, fig. 89; Holttum, R.E. 1964. Flora of Malaya. Orchids: 95-96, fig. 16c.

V. griffithii Rehb. f. var. *ronoensis* (Hayata) S.S. Ying = *V. somai*

43. *V. guianensis* Splitg. in Ann. Sci. Nat. Bot. s. 2, 15: 279 (1841). Type: Surinam, *Splitgerber 409* (holo. P?).

?*V. surinamensis* Rehb. f. in Ned. Kruidk. Arch. 4: 321 (1859). Type: Based upon same type as *V. guianensis* Splitg.

V. acuta Rolfe in J. Linn. Soc. Bot. 32: 453 (1896). Type: Surinam, Marowynne, Aug. 1846, *Kappler* (holo. K-LINDL!).

V. latisegmenta Ames & C. Schweinf., Sched. Orchid. 8: 2 (1925). Type: Guyana (British Guiana), Upper Rupununi River, near Dadanawa, 29 May 1922, *de la Cruz 1404* (holo. AMES 22973!; iso. GH 7850!).

DISTRIBUTION: Guyana, Surinam, and Brazil.

Vanilla guianensis has been regarded as an obscure species. Splitgerber, in the original description, mixed a species of the membranaceous group with the fragrant fruits of a penicillate species, perhaps *V. grandiflora*. The illustration that appeared in De Vriese, Tuinb.-Fl. 3: 33. 1856, clearly illustrates the mistake, and it is not accurate with respect to the flower and inflorescence structure, since the inflorescence, if short and with small bracts for a species of the Membranaceous group, is densely-flowered, and the lip is rather deeply 3-lobed.

Rolfe (1896) recognized Splitgerber's mistake and reduced *V. guianensis* to the synonymy of *V. inodora* (his concept including specimens that here we recognize as *V. inodora*, *V. mexicana*, and *V. guianensis*) and considered Reichenbach's proposal of *V. surinamensis* as an error. However, Rolfe described *Vanilla acuta* in the same revision, based on a Kappler specimen and cited a Schomburgk illustration at the British Museum from the Berbice River, as probably belonging to the same species. We agree that Kappler's and Schomburgk's specimens are conspecific, although it is evident that the original description was based upon an open bud, very damaged by the dissection. The very short inflorescence with small bracts, and rather chartaceous texture of leaves are very characteristic for a membranaceous species.

Later, Ames and Schweinfurth (1925) described *V. latisegmenta*. Their description is very good and the

type well-preserved and with analytical drawings and matches very well with the several specimens listed below from the Guyanas and Amazonia.

This is a large flowered species that seems to be very close to *V. mexicana*, but it is distinguished by its much broader lip (45-50 vs. 30 mm broad), which is not as distinctly 3-lobed, but approaching hexagonal with the apical lobe very broadly ovate, or obscurely defined, its few-flowered inflorescence (bearing only 4-5 flowers), shorter than 10 cm, usually 4-5 cm long and the small, ovate, acuminate bracts. *Vanilla martinezii* from Guatemala has also a subentire, very broad lip, but in this species the veins are warty in the basal half, and the raceme is longer. In dried specimens the very broad lip in which veins are strongly marked is very distinct.

COLLECTIONS: BRAZIL: *Huber s.n.* (BM! MG 1864!); *Huber 1864* (G 78889/105!); Photo of plant in habitat, Arboretum amazonicum (as *V. aromatica* Sw.) (K). GUYANA: *Schomburgk s.n.* (BM NY! photo, K! tracing from drawing at BM); Kaituma River, M.W.D. 211 (K!); *Im Thurm 64* (K!); *Jenman 689* (K!); *Jenman 1614* (K!); *Barkley s.n.* (K! painting). SURINAM: *Hostmann 71* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 255, fig. 115 (as *V. acuta*); Werkhoven, M. 1986. Orchids of Suriname: 228, 236 (as *V. mexicana* Mill.).

44. *V. hallei* Szlach. & Olszewski in Fl. Cameroun 34: 282 (1998). Type: Gabon, Belinga, *N. Hallé 3065* (holo. P!).

DISTRIBUTION: Endemic to Gabon.

This species is closely related to *V. africana*. However, the lip is fleshier, fused to the column in the basal 1/4, and with papillae in the disc rather than long bristles.

45. *V. hamata* Klotzsch in Bot. Zeitung (Berlin)-55: 563 (1846). Type: Peru, *Pavón s.n.* (holo. B †, photo. AMES 38629! sterile, iso. BM! G 7889/123 124, W!).

DISTRIBUTION: Endemic to Peru.

We have dissected floral buds (not attached to an inflorescence) at G and BM. It is a species of the *V. pompona* group, with large tepals (e.g. petals at least 63 × 8 mm), with a rather smooth lip, a callose, penicillate callus, and a thickened axial cushion in the apical

part of the lip. The lip is trilobed, with the midlobe projecting and perhaps emarginate. However, it seems to be distinct from all the known species in that group, particularly by the widely elliptic, rounded leaves.

Another, well-preserved bud from the G specimen is perhaps an *Epistephium* species, because of its numerous retrorse hairs and lip scarcely fused to the column.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 233; Schweinfurth, C. 1958. Orchids of Peru 1: 42-43. Fieldiana: Botany 30.

46. *V. hartii* Rolfe in Bull. Misc. Inform. Kew 1899 (151/152): 133 (1899). Type: Trinidad, Cabasterre Arima, *Hart 6355* (holo. K!; iso. AMES 67785!).

V. leprieurii Portères in Bull. Soc. Bot. France, 98: 94. 1951. Type: French Guyana, Cayenne, 1846, *Leprieur s.n.*, (holo. P not seen, drawing!).

DISTRIBUTION: Mexico to Brazil and French Guyana.

Vanilla hartii is an interesting species with a weak vegetative habit similar to that of *V. bicolor*. However, it presents flowers, and especially a penicillate callus with the structure of the *V. planifolia* group, with which it has been confused.

Vanilla leprieurii is considered here to be a synonym of *V. hartii*. Portères (1954) stressed that his *V. leprieurii* was distinct because the nervation in the center of the lip is denser, with the zone before the nervation thicker, more imbricated scales in the penicillate callus, and the apex of the lip more emarginate, apiculate and pleated.

Vanilla hartii has not been previously reported from Brazil, but we have a herbarium specimen and two unidentified leaf samples whose ITS DNA sequences indicate that they belong to *V. hartii*. The collections from Costa Rica are very stout.

COLLECTIONS: COSTA RICA: *Grayum 7998* (MO!). HONDURAS: *Standley 52824* (AMES!). BELIZE: *Davidse 36251* (BM!). TRINIDAD & TOBAGO: *Britton 2841* (AMES!); *Broadway s.n.* (AMES! in part K!); *Fendler 1007* (BM! K!). DOMINICA: *Hodge 387* (AMES! sterile). BRAZIL: *Rabelo & Pen 720* (MG! sterile).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 248, fig. 12 (as *V. leprieurii*) and 250-251, fig. 113; Schultes, R.E. 1960. Native Orchids of Trinidad and Tobago: 39.

47. *V. havilandii* Rolfe in Bull. Misc. Inform. Kew 1918: 236 (1918). Types: Sarawak, Kuching, *Haviland s.n.* (syn. K!); Sarawak, Matang, *Ridley s.n.* (syn. K!).

DISTRIBUTION: Borneo.

A species somewhat similar to the Javanese *V. albida*, but with congested, many-flowered inflorescences bearing pendent flowers, apparently with flared tepals. The oblong-elliptic, long-acuminate leaves are rather thin in substance.

COLLECTIONS: MALAYSIA: SARAWAK, *BROOKE 8181* (G 7889/181!); *LAMB SAN 89632* (K!); *SANDS ET AL. 3702* (K!); *CHAN 927* (K!, DRAWING). INDONESIA: KALIMANTAN, *AFRIASTINI 310* (K!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 209-210.

48. *V. helleri* A.D. Hawkes in Phytologia 14 (1): 19, t. 13. (1966). Type: Nicaragua, Dept. Chontales, 2 miles S of La Libertad on the road to Santo Tomás, 1900 ft, April 1962, *Heller 7946* (holo. AMES not located; iso. SEL!).

DISTRIBUTION: Nicaragua and Costa Rica.

This is one the rarest of the Central American *Vanilla* species. It has relatively small flowers with a distinct 3-lobed lip, in which the midlobe is covered with retrorse, complanate, elongate trichomes, resembling in some way the South American *V. ribeiroi*. It is a member of the *V. odorata-V. insignis* complex, also with retrorse, orange trichomes on the midlobe.

COLLECTIONS: COSTA RICA, *Davidse & Pohl 1503* (F!).

SOURCES: Hamer, F. 1984. Ic. Pl. Trop. Pl. 1192; Hamer, F. 1990. Orch. Centr. Amer. Selbyana 11: 847.

49. *V. heterolopha* Summerh. in Bull. Misc. Inform. Kew 1938: 149 (1938). Type: Gabon, Upper Ogoué River, Matoro, Oct. 1929, *Le Testu 7494* (holo. P!; iso. BM! K!).

DISTRIBUTION: Gabon and Congo.

This species is a member of the *V. africana* group, resembling vegetatively *V. africana*, but it is easily distinguished by its truncate, rectangular, sharply recurved midlobe of the lip, and warts and papillae in the center of the blade. When flattened, the midlobe of the lip appears slightly broader towards the apex. In the other members of the *V. africana* group, the apical

lobe of the lip is acute to acuminate, with retrorse, fimbriate scales, rather than warts.

COLLECTIONS: GABON: *Le Testu 5769* (BM! K drawing!); *Le Testu s.n.* (K!); *Le Testu 7494bis* (BM!). SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 206-207, fig. 96; Szlachetko, D.L. & S. Olszewski. 1999. Fl. de Cameroun: 282, pl. 100, G-M.

V. hirsuta M.A. Clem. & D.L. Jones = *V. × tahitiensis*

50. *V. hostmannii* Rolfe in J. Linn. Soc. Bot. 32: 462 (1896). Type: Surinam, *Hostmann 306* (holo. K!, iso.K-LINDL!).

?*Vanilla planifolia* var. *gigantea* Hoehne, Com. Lin. Tel. Est. M.G. Amazonas, Bot. 1: 217 (1910). *V. barrereana* Veyret & Szlach. in Bull. Mus. Natl. Hist. Nat., B, Adansonia 16 (2-4): 220 (1995). Type: French Guiana, *Cremers 4523* (holo. P, iso. CAY).

V. porteresiana - Szlach. & Veyret in Bull. Mus. Natl. Hist. Nat., B, Adansonia 16 (2-4): 219 (1995). Type: French Guiana, *Oldeman 2087* (holo. P).

DISTRIBUTION: Colombia, Guyana, French Guiana, Surinam, Venezuela and Brazil.

Vanilla hostmannii is a member of a small group of species that includes also *V. cribbiana*, *V. dressleri*, and *V. weberbaueriana*, characterized by the conspicuously distichous arrangement of the basal bracts, its entire to obscurely trilobed lip adorned with thickened, papillose veins on the lip apex, and with the ovary, sepals and the petals keels oddly granulose. From them is distinguished by its many-flowered racemes, larger leaves, a more thickly veined lateral lobes of the lip. It has cream-colored flowers.

Vanilla barrereana and *V. porteresiana*, described by Veyret & Szlachetko (1995), have the characteristic thickened veins and granulose sepals surface but have smaller measurements and different lip tips. We have compared them with immature buds of *V. hostmannii* and we believe than they are better considered synonyms of *V. hostmannii*. Several specimens of *V. hostmannii* have been annotated as *V. planifolia* var. *gigantea*, but we have been unable to locate the type specimen of this variety to confirm if it is a synonym of *V. hostmannii* or of *V. grandiflora* (= *V. pompona* sensu Hoehne), as stated by Hoehne in 1945.

Vanilla hostmannii seems to be a common species in Guyana and the Amazon.

COLLECTIONS: GUYANA: *Anderson 71* (K!); *Jenman 89 & 6390* (K!); *im Thurn 65* (K!). COLOMBIA: *Lehmann H.K. 1187* (K!); *Schultes 3809* (AMES!). BRAZIL: Acre, *Prance 7955* (MG!); Para, *Wulfschlaegell s.n.* (W!); *Prance et al. P25739* (K! MG!); *Maciel & Santos 1939* (MG!). Amazonas, *Silva & Brazão 60960* (VEN!). VENEZUELA: *Wurdack & Adderley 43074 & 43170* (VEN!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 193; Hoehne, F.C. 1945. Flora Brasílica 12, 2: Orchidaceae: 18.

51. *V. humblotii* Rchb. f. in Gard. Chron. n.s. 23: t. 726 (1885). Type: Grande Comore, *Humblot 1413* (holo. W!, iso. BM! K! P!).

DISTRIBUTION: Comoros Islands.

Another member of the *V. roscheri* group distinguished by its yellow flowers with dark maroon marks in the throat of the lip.

COLLECTIONS: COMOROS: Mayotte, *Labat 2905* (P, K!). SOURCES: Rolfe, R.A. 1905. Bot. Mag. t. 7996; DuPuy, D. Cribb, P., Bosser, J. & Hermans, J. & C. 1999. The Orchids of Madagascar: 207.

52. *V. imperialis* Kraenzl. in Notizbl. Bot. Gard. Berlin-Dahlem 1: 155, t.1 (1896). Type: Cameroon, Yaoundé, *Zenker & Staudt 626* (holo, B†).

V. lujae De Wild., Belg. Colon. 10: 28 (1904). Type: Zaire, *Luja s.n.* (holo. BR).

V. grandifolia Lindl. var. *lujae* (De Wild.) Geerinck in Bull. Soc. Roy. Bot. Belgique 107, 1: 58 (1974).

V. imperialis Kraenzl. var. *congolensis* De Wild. in Rev. Hist. Nat. Appl. (Paris) 2: 188 (1921). Type: Zaire, Dundusana, *Mortehan 244* (holo. BR).

DISTRIBUTION: Sierra Leone, Ivory Coast, Ghana, Nigeria, Cameroun, Democratic Republic of the Congo, Angola, Uganda, United Republic of Tanzania, Kenya.

This common African species has the most spectacular flowers in the genus, which are big, ivory-white, heavily veined-blotched with deep rose to purple. The inflorescence has many imbricate bracts, resembling some species of *Costus*, however, many specimens from East Africa have shorter bracts. It is

closely related to *V. ochryae* and to *V. polylepis* (see comments under the species).

COLLECTIONS: CAMEROUN: *Bates 1523* (BM!). GHANA: *Westward 113, 226* (K!); *Vigne 2412* (K!); *Hall GC 35391* (K!). SIERRA LEONE: *Assi 9041* (K!); *Jaeger 40* (G 78889/184 185!); *Jaeger 16566* (K!). NIGERIA: *Chapman 4869* (K!). UGANDA: *Eggeling 2062* (K!); *Dümmer 2672* (K!), *2672A* (BM!) *Eggeling 1065* (K!); *Ussher 83* (K!); *Poulsen et al. 971* (K!); *Bagshawe & Camb 1142* (BM!); *van Someren E.A.H. 11163* (EAH, K). TANZANIA: *Moreau 429* (K!); *Greenway 6664* (K!); *Greenway 2928* (K!). ANGOLA: *Rep. de Agricultura 14214* (K!); *Gosswiller 13837* (BM!).

SOURCES: Rolfe, R.A. 1897. *Flora Trop. Afr.* 7: 178; Robyns, F.H. & R.L. Tournay. 1955. *F.P.N.A.* 3: 454; Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 174-176, fig. 84 and 178-179 (as *V. lujae*); Summerhayes, V.S. 1968. *Flora of West Tropical Africa* 3(1): Orchidaceae: 205-206; Piers, 1969. *Orch. E. Afr.* ed. 2: 82, fig. 26; Cribb, P. 1984. *Flora of Tropical East Africa. Orchidaceae* 2: 259-261; Geerinck, D. 1984. *Flore D'Afrique Centrale (Zaire, Rwanda-Burundi)*: 244-246; Stewart, J. 1996. *Orchids of Kenya*: 89; Szlachetko, D.L. & S. Olszewski. 1999. *Fl. de Cameroun*: 290-291, pl. 103, A-E.

53. *V. inodora* Schiede in *Linnaea* 4: 574 (1829). Type: Mexico, *Schiede s.n.* (holo. BM!, iso. LE, W!).

V. preussii Kranzl. in *Notizbl. Bot. Gard. Berlin-Dahlem* 7(67): 320 (1919). Type: Guatemala, *Preuss 1445* (holo. B†).

V. pfaviana Rechb.f. in *Gard. Chron.* n.s. 20: 230 (1883). Type: Costa Rica, *Pfau s.n.* (holo. W!).

DISTRIBUTION: Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica and perhaps Panama.

This is the species of the membranaceous group with most northern distribution. It is distinguished by the high, thick cushion-like, axial callus of its emarginate lip.

COLLECTIONS: MEXICO: *Liebman 297* (K!); *Liebman 284-296* (BM!); *Liebman 7268* (BM!); *Calzada 01031* (BM!). Veracruz, *Nagel in Oestlund 2683* (AMES!); *Purpus in Oestlund 4876* (AMES!); *Purpus in Oestlund 5045* (AMES!); *Purpus 8481* (AMES!). Puebla, *Arsène 1682* (AMES!); Guerrero:

Nagel in Oestlund 1984 (AMES!), *1985* (AMES! BM!); Chiapas: *Matuda 17912* (AMES!). BELIZE: *Gentle 1672* (AMES!). GUATEMALA: *Steyermark 49171* (AMES!). HONDURAS: *Yuncker et al. 8335* (AMES!). COSTA RICA: *Skutch 2592* (AMES! K!); *Lankester K331* (K!); *von Wedel 1423* (BM!).

SOURCE: Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 252-253 (mixed with *V. mexicana*) and 257 (as *V. pfaviana*).

54. *V. insignis* Ames in *Bot. Mus. Leaflet* 2: 101 (1934). Type: Honduras, *Edwards 407* (holo. AMES 40085!).

DISTRIBUTION: Mexico, Guatemala, Belize, Honduras, reported by Dressler (1993) for Costa Rica.

This common Mesoamerican species has rarely been collected in flower. Its flowers with large apple green tepals and a cream-colored lip bearing orange-ochre retrorse papillae are characteristic. Sterile plants can be distinguished by their sulcate stems with minutely papillose surface. It is a member of the *V. odorata* group, but it has shorter leaves and more xerophytic habit.

COLLECTIONS: MEXICO: Oaxaca, *Nagel in Oestlund 4584* (AMES!); Veracruz, *Nagel in Oestlund 2682* (AMES!); *Purpus in Oestlund 4866* (AMES!); *Purpus in Oestlund 5961* (AMES!); Quintana Roo, *Nagel in Oestlund 4973* (AMES!). BELIZE: *Gentle 1063* (AMES!). GUATEMALA: *Steyermark 45233* (AMES!).

SOURCES: Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 231-233, fig. 107. Dressler, R.L. 1993. *Field Guide to the Orchids of Costa Rica and Panama*.

55. *V. kaniensis* Schltr. in *Repert. Sp. Nov. Regni Veg. Beih.* 1: 32 (1911). Type: Papua New Guinea, *Schlechter 17634* (holo. B†; published drawing!).

DISTRIBUTION: Bismarck Mountains, Papua New Guinea.

Similar to *V. kempteriana* and *V. wariensis*, but with smaller (20-25 × 4-7 cm) leaves.

SOURCES: Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 221; Howcroft, N.H.S. 1984. *A Guide to the monocotyledons of Papua New Guinea*. R.J. Johns & Hay, A.J.M. (eds.) 4. *The Orchidaceae* (in part): Forestry Department PNG, University of Technology. p. 126, fig. 72; O'Byrne, P. 1994. *Lowland Orchids of Papua New Guinea*. SNP Ltd. p. 9.

56. *V. kempteriana* Schltr. in Repert. Sp. Nov. Regni Veg. Beih. 1: 32 (1911). Type: New Guinea, *Schlechter 18045* (holo. B †; published drawing!; iso.G!).

DISTRIBUTION: Papua New Guinea, between Lae and Madang.

Distinguished from other species from the island by its rather broad leaves.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 220-221; Howcroft, N.H.S. 1984. A Guide to the monocotyledons of Papua New Guinea. R.J. Johns & Hay, A.J.M. (eds.) 4. The Orchidaceae (in part): Forestry Department PNG, University of Technology. p. 126, fig. 73; O'Byrne, P. 1994. Lowland Orchids of Papua New Guinea. SNP Ltd. p. 9.

57. *V. kinabaluensis* Carr in Gard. Bull. Straits Settlements: 176 (1935). Types: Borneo, *Carr 3157* (syn. K!); Kadamaian (Tampasuk) River, at the entrance to Menetendok Gorge, c. 2,700 feet, March 1933, *Clemens 26300* (syn. BM!); Dallas, 3,000 feet, Aug. 1931; *Clemens 26725* (syn. BM! K!); Dallas, 3,000 feet, 15 Sept. 1931, *Clemens* (syn. K).

DISTRIBUTION: Borneo (Sabah) and Peninsular Malaysia.

Very similar to the Bornean *V. abundiflora* J.J. Sm., but with larger flowers, a more distinctly 3-lobed lip with a median keel and without irregularly seriate warts. The column lacks the appendages found in *V. abundiflora*. It is recognized by its extremely long raceme, sometimes with up to 165 flowers, which open successively perhaps during much of the year.

COLLECTIONS: MALAYSIA: Sabah, *SFN-25273* (K!); *Joseph & Donggop SAN 128637* (K!); *Wood 909* (K!, and drawings); *Lamb 1230/90* (K!); *Lugas 1724* (K!); *Burbidge s.n.* (BM! K drawings!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 216; Holttum, R.E. 1964. Flora of Malaya. Orchids: 96-97.

V. klabatensis Schltr. *nomen nudum*.

V. latisegmenta Ames & C. Schweinf. = *V. guianensis*

V. laurentiana De Wild. = *V. crenulata*

V. leprieurii Portères = *V. hartii*

V. lindmaniana Kraenzl. = *V. palmarum*

V. lujae De Wild. = *V. imperialis*

V. lutea C.H. Wright ex. Griseb. = *V. palmarum*

V. lutescens Moq. ex Dupuis = *V. grandiflora*

58. *V. madagascariensis* Rolfe in J. Linn. Soc. Bot. 32: 476 (1896). Type: Madagascar, Bomatoe Bay, *Bojer s.n.* (holo. K!).

DISTRIBUTION: Madagascar.

Vanilla madagascariensis is very similar to *V. phalaenopsis* from the Seychelles and *V. roscheri* from E Africa. All three have large, white flowers with pink to apricot throat to the lip, but they differ in the lip lobing. They have some of the most spectacular flowers in *Vanilla*.

SOURCES: Du Puy, D., Cribb, P. Bosser, J. & Hermans, J. & C. 1999. The Orchids of Madagascar: 207, pl. 42B, 43C.

V. majaijensis Blanco = ?*V. planifolia*

V. marowynensis Pulle = *V. appendiculata*

59. *V. martinezii* Soto Arenas, ined.

DISTRIBUTION: Guatemala, expected from Belize and Honduras.

V. martinezii is member of the *V. mexicana* group. The most similar species is *V. guianensis*, however in *V. guianensis* the callus is formed by 5 basal keels and 3 rather prominent ones, but not or almost not verrucose, and the lip apex is trilobed. *V. martinezii* seems to be endemic of the wet lowlands around Lake Izabal.

60. *V. methonica* Rchb. f. & Warsz. in Bonplandia 2: 97 (1854). Type: Colombia (New Granada), 6-8000ft., *Warszewicz s.n.* (holo. W19363!; iso. K-LINDL!).

DISTRIBUTION: Colombia and Peru, apparently only on the eastern slopes of the cordillera.

We have seen very few specimens referable to this species, and the type is poorly preserved. However, the protologue is good enough to identify their specific concept with modern specimens from Peru.

The rather short inflorescences (for the membranaceous group), with small, broadly ovate bracts and the large flowers with a strongly 3-lobed lip, in which the lateral lobes are oblong and rounded and the emarginate midlobe are characteristic. Like many others in the *V. mexicana* group, it has 3 longitudinal keels, converging on the lip apex, but the keels are thickened in the distal part and somewhat rugose. It

seems to be more closely related to *V. inodora*, but it lacks the characteristic cushion-like, massive callus of that species.

V. oroana Dodson, from the Pacific slopes of Ecuador, has very large foliaceous bracts, the tepals are strongly contorted, and it has 5 apical keels on the acute lip; no other membranaceous vanilla is known from Andean South America.

COLLECTIONS: COLOMBIA: *Barragán in Lehmann HK1181* (K!); *Goudot s.n.* (W sketch!). PERU: *Smith 3883* (MO!); *Vargas 18697* (AMES!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 254-255.

61. *V. mexicana* Mill., Gard. Dict. (ed. 8), no. 1 (1768). Type: Haiti, *Plumier s.n.* (holo. Plumier's original drawing at P; reproduced in Plumier, Nov. Pl. Amer. Genera 25, pl. 28, 1703!).

Epidendrum vanilla L., Sp. Pl. 2: 952 (1753).

Type: "Volubilis siliquosa plantaginis folio" in Catesby, Nat. Hist. Carolina 2 (?): app. t. 7. 1747; lecto. designated by Cribb in Cafferty & Jarvis, Taxon: 48(1): 47. 1999.

V. aromatica Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 66 (1799). Type: based on same type as *Epidendrum vanilla* L.

V. anaromatica Griseb., Fl. Brit. W. Ind. 638 (1864). Type: Based upon Plumier, Ed. Burm., t. 188.

V. epidendrum Mirb., Hist. Nat. Pl. 9: 249 (1802-6).

V. vanilla (L.) Huth in Helios 11(9): 136 (1893).

DISTRIBUTION: U.S.A. (Florida), Cuba, Puerto Rico, Hispaniola, Lesser Antilles, Trinidad and Tobago, perhaps N. South America (Venezuela). Reported repeatedly from Guianas and Brazil, but the examined material belongs to *V. latisegmenta* or other taxa.

The taxonomic history of this species is very confusing. Mexican specimens referred to this species belong to *V. inodora*. Its lip is 3-lobed, the midlobe is well-developed and can be subacute to rounded. It is closely related to *V. costaricensis* with a truncate lip, to *V. ovata* and *V. martinezii* with larger flowers, and the latter with many warts near the base of the lip.

Some authors have considered *V. inodora* as the valid name of this species. Although the type of *V. inodora* is lacking flowers, there is abundant material from the original area to establish that it is the species

common in Mesoamerica that has a thick, longitudinal cushion-like callus and is widely known as *V. pfaviana*. The West Indies taxon with a callus formed by 3 longitudinal keels it is unknown in Mexico.

COLLECTIONS: PUERTO RICO: *Sintenis 1739* (K!); *Sintenis 2456* (AMES!); *Sintenis 2486* (G 7889/104, /107!); *Sintenis 5469* (AMES! BM! G 7889/128! K!); *Eggers 1076* (G 7889/ 178!); *Eggers 1322* (K!); *Kevorkian 6468* (AMES!). CUBA: *Wright 3353* (AMES! K!); *Alain & Acuña 2295* (AMES!); *Clemente 2401* (AMES!); *Britton & Wilson 5221* (AMES!); *Schafer 3211* (AMES!), *3299* (AMES!) & *7982* (AMES!); JAMAICA: *Purdie s.n.* (K!); *Morris 451* (K!); *Wood s.n.* (BM tracing!). TRINIDAD AND TOBAGO: *Baker 14732* (K!); *Britton & Howell 2847* (K!); *Britton & Howell s.n.* (AMES!); *Broadway 3874* (K!); *Crueger s.n.* (K!); *Freeman s.n.* (AMES!); *Simmonds 334* (AMES!); *Britton 2945* (AMES!); *Row & E.E.C. 11332* (AMES!). GUADELOUPE: *Smith 10350* (AMES!). DOMINICA: *Immary 138* (K!); *Ramage s.n.* (K!); *W.H. and B. T. Hodge 3671* (AMES!); *Ernst 1462* (AMES!). ST. LUCIA: *Proctor 17710* (AMES!). DOMINICAN REPUBLIC: *Eggers 2086* (K!). HAITI: *Eyerdam 395* (AMES!); *Zanoni & García 42003* (AMES!). MARTINIQUE: *Duss 2081* (AMES!).

SOURCES: León, F.S.C. & F.S.C. Alain. 1946. Flora de Cuba I: 351 (as *V. inodora*); Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 252-253 (mixed up and as *V. inodora*); Schultes, R.E. 1960. Native Orchids of Trinidad and Tobago: 40 (as *Vanilla inodora*); Kenny, J. 1988. Native Orchids of the Eastern Caribbean: 22; Acuña, G.J. 1939. Catálogo Descriptivo de las Orquídeas Cubanas: 21 (as *V. inodora*); Dunsterville, G.C.K. & L.A. Garay. 1959. Venezuelan Orchids Illustrated 1: 432-433 (as *V. inodora*); Foldats, E. 1969. Flora de Venezuela. Orchidaceae I: 118, fig. 39 (as *V. inodora*); Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 174; Cafferty & Jarvis, Taxon: 48(1): 47. 1999. Lectotypification of *Epidendrum vanilla*.

V. microcarpa H. Karst., Deut. sehe Fl. 458 (1880-83).

Type: Venezuela

Poorly known species.

V. montagnacii Portères in Bouriquet, Vanillier et Vanille 46: 282 (1954), *nom. inval.* Based upon:

Madagascar, *P.R. Montagnac 146* (not seen)

This species has an entire lip with two subpapillose keels on its disc. It is possibly a semi-peloric form of *V. decaryana* or *V. madagascariensis* which are both found in the region. Portères failed to provide a Latin description of this name which is consequently invalid. COLLECTIONS: MADAGASCAR: N of Morondava, *Bosser 18187* (P!); *Abraham 78* (P!).

62. *V. montana* Ridl. in J. Fed. Malay States Mus. 6: 58 (1915). Type: Malaya, Perak, Gunong Kerbau, 4400 - 5500 ft, 19 March 1913, *Robinson s.n.* (holo. K!; iso. AMES 25073! BM!).

DISTRIBUTION: Malaysia.

Seidenfaden considered this species to be conspecific with Thai plants identified by him as *V. albida*, but thought by us to be *V. yersiniana*. However, it differs from *V. yersiniana* by the much longer hairs at the lip apex (up to 4 mm long) and much broader leaves. It seems to be a rare plant and as far as we know it is only known from the type specimen.

SOURCES: Ridley, H.N. 1924. The Flora of the Malay Peninsula: 201; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 222; Holttum, R.E. 1964. Flora of Malaya, ed. 3. Orchids: 97.

63. *V. moonii* Thwaites, Enum. Pl. Zeyl. 312 (1864). Type: Sri Lanka, *Thwaites 3204* (holo. K!; iso. AMES 71375! BM! G!).

DISTRIBUTION: Endemic to Sri Lanka.

This species has 2 rows of papillae at the apical lobe of the lip, in the way of many other Asian species. The simple raceme, with many (up to 21) flowers on a thick rachis is also characteristic.

COLLECTIONS: SRI LANKA: *Wight s.n.* (K!); *Champion* (AMES! K-LINDL!); *collector 1869* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 182; Jayaweera, D.M.A. 1981. Orchidaceae. A Revised Handbook to the Flora of Ceylon 2: 333.

64. *V. nigerica* Rendle, Cat. Pl. Oban 108 (1913). Type: S. Nigeria, Oban, 1911, *Talbot 776* (holo. BM!).

DISTRIBUTION: Nigeria and Cameroon.

A species of the *V. chalottii* group. It is similar to *V. seretii*, both being characterized by their narrowly oblong leaves, verrucose stems and pretty, large, white and pink flowers with the hollow saccate lip typical

of the *V. chalotti* group. *Vanilla nigerica* is different from *V. seretii* in its lip being provided with 2 gibbae at base, the coarsely hairy lip throat, and the recurved, not rolled midlobe of the lip. It is probably a rare plant.

COLLECTION: CAMEROON: *Bates 1263* (BM!). SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 172; Summerhayes, V.S. 1968. Flora of West Tropical Africa 3(1): Orchidaceae: 205-206.

65. *V. ochyrae* Szlach. & Olszewski in Fl. Cameroun 34: 291 (1998). Type: Cameroon, *Jacques-Félix 4727* (holo. P!; iso. K!).

DISTRIBUTION: Cameroon.

A species closely related to *V. imperialis*, but distinguished by its clearly trilobed lip, with a semiorbicular midlobe larger than the larger lateral lobes and the margins undulate. The lamellae and trichomes of the lip are branched.

COLLECTION: CAMEROON: *Endeguele 113* (K!).

66. *V. odorata* C.Presl, Reliq. Haenk. 1(2): 101 (1830). Type: Ecuador, *Haenke s.n.* (holo. PR!; iso. PR!).

V. ensifolia Rolfe in Bull. Misc. Inform. Kew 1892(65/66): 141 (1892). Type: Colombia, *Goudot s.n.* (holo. K!).

V. uncinata Huber ex Hoehne in Arquiv. Inst. Biol. (S. Paulo) 8: 269 (1937). Type: Pará, Brazil, *Goeldi 7392* (holo. MG!).

V. denticulata Pabst, 23rd Congr. Nac. Bot., Garanhuns: 109 (1972). Type: Brazil, *Ferreira 37-67* (holo. HB).

DISTRIBUTION: Mexico, Guatemala, Costa Rica, Panama, Colombia, Peru, Bolivia, Brazil.

Vanilla odorata is widely distributed in continental tropical America, from Mexico to Bolivia. It is easily distinguished by its narrowly lanceolate, long acuminate leaves; although specimens grown in shaded spots may have broader leaves. Its fruits are strongly fragrant and are collected from wild plants in many areas of Latin America. It is occasionally grown in Oaxaca, Mexico, as source of vanilla fragrance.

Vanilla denticulata and *V. uncinata* seem to be conspecific with it, their vegetative and floral dimensions falling within the known range of *V. odorata*, although the lip of *V. uncinata* is slightly emarginate. *Vanilla fimbriata* is also very closely related but the flowers are smaller. However, better

and more abundant material from Amazonia and the Guyanas is necessary to be compared carefully with specimens of *V. odorata* from other areas.

COLLECTIONS: BELIZE: *Whitefoord 1316* (BM!). COSTA RICA: *Standley & Valerio 48917* (AMES!). GUATEMALA: *Aguilar 164* (AMES!). PANAMA: *Hunnewell 16433* (AMES!). COLOMBIA: *Lehmann H.K. 1183* (K!). PERU: *Killip & Smith 29065* (AMES!); *Williams 3161* (AMES!). BOLIVIA: *White 1115, 1821* (AMES!); *Spencer Moore 637a* (BM!). SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 243-245, fig. 110; Schweinfurth, C. 1958. Orchids of Peru I. Fieldiana: Botany 30: 43; Dodson, C.H. & P.M. Dodson. 1980. Ic. Pl. Trop. pl. 353; Hamer, F. 1984. Ic. Pl. Trop. t. 1193; Dodson, C.H. & H.H. Gentry. 1985. La Flora de Jauneche: 110, t. 44-A; Garay, L.A. 1978. Flora of Ecuador. Orchidaceae 1: 49, fig. 14.

67. *V. organensis* Rolfe in J. Linn. Soc. Bot. 32: 452 (1896). Types: Brazil, Organ Mountains, *Gardner 632* (lecto. K-LINDL!, here designated; isolecto. AMES 71366! G! K! W 19645!) *Miers* (syn. BM! K!); Near Rio de Janeiro, *Glaziou 11620* (syn. K!) & *14320* (syn. K!).

A membranaceous *Vanilla* which seems to be closely related and perhaps not distinct from *V. parvifolia*, except for its more ruffled tepals, a trait that is very variable in other membranaceous vanillas. *V. edwallii* and *V. bertonensis* are allied, but both have a long acuminate lip.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 257, fig. 116; Pabst, G.F.J. 1966. As Orquídeas do Estado da Guanabara. Orquídea 28(2-6): 169-170.

68. *V. oroana* Dodson in Orquideologia 22(3): 210 (2003). Type: Ecuador, Prov. El Oro, 3.7 km N of junction of old and new roads from Piñas to Santa Rosa, 12 km west of Piñas, 1400 m, 19 Apr 1989, *Dodson, Williams, Dressler, Whitten & Embree 17951* (holo. AMES!; iso. K! (sterile) MO!).

DISTRIBUTION: Known only from the type collection in western Ecuador.

Vanilla oroana is a member of the membranaceous group. It is a large vine, flowering at apex up to 18 m tall, with a very long inflorescence bearing large

foliaceous bracts up to 110 × 65 mm. The large flowers have contorted tepals and the lip is covered with papillae and the apex is 5-keeled. Its sepals and petals are green, and its lip white, with yellow-orange lamella on apical lobe. Its nearest relatives seem to be the members of the *V. mexicana* complex.

V. ovalifolia Rolfe = *V. zanzibarica*

69. *V. ovalis* Blanco, Fl. Filip. 448 (1845). Type: Philippines, Mt Majajjai, Lilio, *Azaola s.n.* (not located).

Epidendrum vanilla sensu Blanco, Fl. Filip. (ed. 2) 643: (1837), non L.

V. majajjensis Blanco, loc.cit. 593 (1845).

V. philippinensis Rolfe in J. Linn. Soc. Bot. 32: 459 (1896). Type: Philippine Islands, without precise locality, *Cuming 2132* (holo. K!; iso. BM!).

DISTRIBUTION: The Philippines (Luzon, Mindanao, Leyte, Samar and Sibuyan Islands).

This is the only leafy *Vanilla* in the Philippines. Its sepals and petals are greenish-cream and the lip is marked with purple lines. It is apparently related to *V. platyphylla* from Sulawesi and to the New Guinean species, but it is distinguished by its very hairy lip apex.

COLLECTIONS: *Cuming* (K-LINDL!); Luzon, *M. Perrotet s.n.* (G 7889/103!); *D.E. Elmer 16035* (BM! G 7889/110! K!); *A.D.E. Elmer 9259* (BM! K!); *H.G. Gutiérrez 78082* (K!); *A. Loher 5420* (K!), *5421* (K!) *5422* (K!); *J.S. Serrato s.n.* (BM! K!); *Irosin 16035* (BM!); *Merrill 665* (BM! K!); Sibuyan, *D.A. Madulid 6875* (K!).

SOURCES: Ames, O. 1908. Orch. 2: 47 (as *V. philippinensis*); Merrill, 1914. Species Blancoana: 459; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 182-183; Valmayor, H.L. 1984. Orchidiana Philippiniana 1: 322.

70. *V. ovata* Rolfe in J. Linn. Soc. Bot. 32: 451 (1896). Type: Guyana, *Martin s.n.* (holo. BM, tracing at K!).

DISTRIBUTION: Venezuela and Guyana.

This is perhaps not different from *V. mexicana*. We have not located the type specimen, and the rough tracing at K is inadequate to be sure. Illustrations identified as *V. mexicana* from South America (e.g. Garay & Dunsterville, 1959) have an unusually broad midlobe to the lip, and may deserve specific

recognition. Another specimen illustrated by Hoehne (1945) and identified as *V. ovata* has very slender segments and narrow midlobe of the lip. We cannot be sure of the identity of the South American material until specimens have become available to us.

COLLECTIONS: VENEZUELA: Delta Amacuro: cf. *J.A. Steyermark 87393* (G 7889/130!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 254 and 264; Dunsterville, G.C.K. & L.A. Garay. 1959. Venezuelan Orchids Illustrated 1: 432; Hoehne, F.C. 1945. Flora Brasiliica t. 29.

71. *V. palembanica* Teijsm. & Binn. in Natuurk Tijdschr. Ned. Indie 29: 243 (1867). Type: Sumatra, *Teijsman* (holo. L).

DISTRIBUTION: Sumatra.

Another scarcely known species that could be related to *V. abundiflora* group.

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 167.

72. *V. palmarum* (Salz. ex Lindl.) Lindl., Gen. Sp. Orch. Pl. 436 (1840). Type: Brazil, Bahía, *Salzmann s.n.* (holo. K-LINDL! iso. K! G 78889/134! LE!).

Epidendrum palmarum Salzmann ex Lindl., Gen. Sp. Orchid. Pl. 436 (1840).

V. lutea C.H. Wright ex Griseb., Cat. Pl. Cub. 267 (1866). Type: Cuba, Wright s.n. (holo. BM?).

?*V. lindmaniana* Kraenzl. in Kongl. Svenska Vetenskapsakad. Handl. 46(10): 17 (1911). Type: Brazil, Matto Grosso, near Palmeiras, Exp. I Regnell, *Lindman 2481* (holo. S).

DISTRIBUTION: Brazil, Venezuela, Guyana, Suriname, Bolivia, Peru. Mostly in the Amazonian basin.

Vanilla palmarum is different from other American *Vanilla* species in lacking a penicillate callus on the lip, and in having its column united to the lip for only about a half of the column length. In other species the penicillate callus is necessary during the pollination, but *V. palmarum* seems to be autogamous. The inflorescence is rather lax, compared with other American vanillas. It forms infrutescences with many thick fruits with a conspicuous calyculus. Weak plants are sometimes confused with those of *V. bicolor*. It is repeatedly reported as growing on palms (*Mauritia*, *Orbignya*, *Attelia*, *Scheelea*, *Syagrus*), and can be very abundant. The mature fruits are apparently odour-less.

Vanilla lindmaniana has been treated as an obscure, doubtful species. However, its habitat, habit, wooly column, simple ecallose lip, and concolorous yellow flowers suggest strongly that it is conspecific with *V. palmarum*. Considering the published drawings, *Vanilla palmarum* is rather variable in the form of the lip.

COLLECTIONS: SURINAME: *Hostmann* (K-LINDL!). BRAZIL: Alagoas, *Gardner 1419* (BM! K!). Maranhao, *Vieira et al. 1545* (CEN 013782!). Tocantins, *Walter et al. 405* (CEN 026289!). Bahia: *Curran 402* (AMES!); *Blanchet s.n.* (G 7889/137,140!); *Blanchet 139* (G 7889/138!); *Vignier s.n.* (G 7889/139!); *Giacometti 878* (CEN 15182!). Goias, *Walter et al. 4100* (CEN 32308, s.n.), *4031* (CEN 32254!), *3698* (CEN 31844!), *2044* (CEN 024613!), *1274* (CEN 17061!) & *973* (CEN 156261!). Mato Grosso, *Prance & Schaller 26301* (CEN 3407, s.n.); *Argent et al. 6349* (K!). Pernambuco, *Ridley et al.* (BM!) *E. Menezes 18* (K!). Para, *da Silva & Santos 30* (MG!); *da Silva et al. 1959* (MG!). Amazonas, *Ribeiro et al. 1333, 1963* (K!). Acre, *Prance et al. 7955* (K!). BOLIVIA: *White 935* (AMES!), *1512* (AMES!), *2332* (AMES!) & *2366* (AMES!); *White s.n.* (AMES 48244!)

SOURCES: Martius, F.P.; 1896. Fl. Brasiliensis 3: pt. 4: 152. 1896; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 260-261, fig. 117; Foldats, E. 1969. Flora de Venezuela. Orchidaceae I: 120-121, fig. 40. Dunsterville, G.C.K. & L.A. Garay. 1976. Venezuelan Orchids Illustrated 6: 438-439. Dodson, C. & R. Vázquez. 1989. Ic. Pl. Trop. II: t. 0395 (as *V. chamissonis*).

V. parishii Rchb. f. = *V. aphylla*

73. *V. parvifolia* Barb. Rodr., Orch. Nov. 2: 271, pl. 36 (1881). Type: Brazil, Paraná Province, near Curitiba, Dec., *Rodrigues s.n.* (holo. RJ†)

V. perexilis Bertoni in An. Ci. Parag. ser. 1. 8: 8 (1910). Type: Paraguay, Puerto Bertoni, *Bertoni 3631* (not seen).

DISTRIBUTION: Paraguay and Brazil (Paraná).

Vanilla parvifolia has a number of closely related species that must be studied carefully when more material become available. It is distinguished from the closely related *V. angustipetala* (syn. *V. rojasiana*), by its broader petals, more defined trilobed lip lacking the papillae or warts on the disc.

Johnson (unpublished manuscript) stated that *V. perexilis* is a small-flowered form of *V. parvifolia*.

SOURCES: Martius, F.P. 1896. Fl. Brasiliensis 3: pt. 4: 151, t. 33. 1896; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 264-266, fig. 119; Johnson, A.E. (unpublished). Las especies argentinas del género *Vanilla*.

V. pauciflora Dressler = *V. trigonocarpa*

74. *V. penicillata* Garay & Dunsterv., Venez. Orch. Ill. 3: 324 (1965). Type: Venezuela, Río Carrao, *Dunsterville* 787 (holo. AMES).

DISTRIBUTION: Venezuela and Brazil.

This is the only leafless *Vanilla* found in the South America. It was described from a specimen with immature buds. Flowering material has larger flowers than those stated in the original description, with greenish-yellow sepals, white petals and a white lip with a yellow center (DS = 57 × 11 mm; LS = 57 × 12 mm, P = 57 × 11 mm, L = 53 × 32 mm, column = 42 mm long; ovary = 30 × 3 mm). It differs from the Caribbean species by its larger flowers, lacking purplish markings, the very long trichomes on the apex of the lip (up to 1 cm long), and the lacerate-fimbriate lateral lobes of the lip. These features and the very long column suggest that it is probably not related to the other leafless American vanillas, but to *V. ribeiroi*, which also has reduced, xerophytic leaves. *Vanilla penicillata* grows in white sand areas and its stems are less than 5 mm thick.

COLLECTIONS: VENEZUELA: *Dunsterville* 786 (K drawing!), 1372 (K published drawing!); *Steyermark & Bunting* 102811 (AMES!). BRAZIL: Amazonas, *Calderón, Monteiro & Guedes* 2675 (K!).

SOURCES: Foldats, E. 1969. Flora de Venezuela. Orchidaceae I: 121, fig. 41.

V. perexilis Bertoni = *V. parvifolia*

75. *V. perrieri* Schltr. in Repert. Sp. Nov. Regni Veg. 33: 114 (1924). Type: Madagascar, Ankarafantsiba, *H. Perrier* 1851 (holo. P!).

DISTRIBUTION: Endemic to Madagascar.

This leafless *Vanilla* is similar to the *V. madagascariensis* complex, but it has yellow flowers with a dark brownish throat of the lip. Its closest relative is *V. humblotii*.

SOURCE: Du Puy, D., P. Cribb, J. Bosser & J. & C. Hermans. 1999. The Orchids of Madagascar: 207-208, pl. 42A.

V. pfaviana Rchb. f. = *V. inodora*

76. *V. phaeantha* Rchb. f. in Flora 48: 274 (1865). Type: Cuba, *C. Wright* 3351 (holo. W; iso. AMES 71001, mixed with cf. *V. poiteai*! BM (another specimen is *V. cf. poiteai*! G 7889/109! K!).

Vanilla planifolia var. *macrantha* Grisebach, Cat. Pl. Cub. 267 (1866). Type: Cuba, *Wright* 3351 (holo. BM?).

DISTRIBUTION: U.S.A. (Florida), Cuba, Jamaica, Lesser Antilles, Venezuela, Trinidad & Tobago, Mexico (Yucatán).

A common leafy species in the Caribbean area. The oblong-elliptic, xerophytic, leaves are usually shorter than the internodes. The flowers are very large, with greenish tepals, and the lip is white with yellow stripes. It is related to *V. bahiana*, from Brazil. From the *V. planifolia* and *V. odorata* complexes can be distinguished by its not warty disc.

COLLECTIONS: U.S.A.: Florida: *Eaton* 1129 (BM! K!). CUBA: *Acuña, Correll & Roig* 18508 (AMES!); *Singleton* 862 (AMES!); *Singleton s.n.* (AMES!); *Hodge & Howard* (AMES!); *Jack* 4775, 5474 (AMES!); *Grey* (AMES!); *Alain & Acuña* 2321 (AMES!); *Britton, Britton & Cowell* 9639 (AMES!). TRINIDAD & TOBAGO: *Rorer s.n.* (AMES!); *Britton & Coker* 555 (AMES!); *Baker* 14733 (K!). JAMAICA: *Harris s.n.* (BM!); *Fawcett* 2 (K!). ST. VINCENT: *Guilding s.n.* (K!); *H.H. & G.W. Smith* 1336 (K!).

SOURCES: León, F.S.C. & F.S.C. Alain. 1946. Flora de Cuba 1: 351; Portères, R. 1954 Le Genre *Vanilla* et ses Espèces: 242-243; Schultes, R.E. 1960. Native Orchids of Trinidad and Tobago: 40; Kenny, J. 1988. Native Orchids of the Eastern Caribbean: 23; Britton, N.L. & C.F. Millspaugh. 1962. The Bahama Flora: 83-84; Acuña, G.J. 1939. Catálogo Descriptivo de las Orquídeas Cubanas: 22. Luer, C.L. 1975. Native Orchids of North America: 70, pl. 18.

77. *V. phalaenopsis* Rchb. f. ex van Houtte, Fl. Serres 17: 97, t. 1769-1770 (1867-1868). Type: Seychelles, *Horne* 607 (holo. W! iso K!).

DISTRIBUTION: Seychelles.

This species is scarcely different from *V. roscheri* from continental Africa and the nearby islands. The appearance is exactly the same, however the base of the lip is said to be much more pubescent than in *V. madagascariensis*.

COLLECTIONS: SEYCHELLES: *Jeffrey s.n.* (K photo!); *Schlieben 16692* (K!); *Thomasset s.n.* (K!); *Fosberg 51988* (K!); *Moulinie & Zelia 731* (K!); *Jeffrey & Zelia 375* (K!).

SOURCE: Reichenbach, H.G. 1877. *Orchidaea Roezlianae Novae*. *Linnaea* 41: 65-67.

V. philippinensis Rolfe = *V. ovalis*

V. pierrei Gagnep. = ?*V. siamensis*

V. pilifera Holttum = *V. borneensis*

V. pittieri Schltr. = *V. pompona*

78. *V. planifolia* G. Jackson in Andrews, Bot. Repos. 8: t. 538 (1808). Type: West Indies, cult. *Greville* (illustration cited here, lecto. selected by Garay, Fl. Less. Antill. 44. 1974).

Epidendrum rubrum Lam., *Encycl.* 1, 1: 178 (1783), *nomen conf.*

V. aromatica Willd. *Sp. Pl.* (ed. 4): 121 (1804), *nomen.*

Myrobroma fragrans Salisb., *Parad. Lond.* 2(1): t. 82 (1807). Type: Illustration cited here.

V. viridiflora Blume, *Bijdr.* 422 (1825). Type: Cult. Buitenzorg BG (holo. not seen).

V. sylvestris Schiede in *Linnaea* 4: 573 (1829). Type: Mexico, Schiede s.n. (holo. BM!).

V. sativa Schiede in *Linnaea* 4: 573 (1829). Type: Misantla, *Schiede s.n.* (iso. BM!).

V. duckei Huber, *Bol. Mus. Paraense Hist. Nat.* 5(2): 327 (1909). Types: Brazil, Amazonas, *A. Ducke 3079* (syn. MG) & *3489* (syn. MG).

V. domestica Druce, *Rep. Bot. Exch. Club* 3: 425. 1913 (1914).

V. rubra (Lam.) Urban in *Repert. Sp. Nov. Regni Veg. Beih* 5: 157 (1920), *nomen conf.*

V. fragrans (Salisb.) Ames, *Sched. Orch.* 7: 36 (1924).

V. bampsiana D. Geerinck in *Bull. Jard. Bot. Belg.* 52, 3-4: 345 (1982). Type: Zaire, Bikoro, Lac Leopold II, Sept. 1930, *Lebrun 1459* (holo. BR!; iso. K!).

V. majajjensis Blanco, *Fl. Filip.* (ed. 2) 593 (1845).

Type. Philippines, Mt. Majajjai, *Azaola s.n.* (holo. not located).

DISTRIBUTION: Native of Mexico, Guatemala, Belize, Honduras, Costa Rica, and Panama. Apparently escaped in Florida, Jamaica, Puerto Rico, Zaire and New Guinea, and perhaps in many other tropical areas.

This species is the cultivated source of the vanilla essence. Its natural range probably ran from Central Veracruz in Mexico to Costa Rica or Panama, but it is now found in many tropical areas as an escape. All the material we have seen from Africa, the West Indies, South America (including Ecuador), and most of Costa Rica and Panama, is indistinguishable from the cv. "Mansa" from Veracruz, and different from wild specimens from Chiapas, Belize and Honduras which have characteristically broad, elliptic leaves.

We have not examined the syntypes of *V. duckei* Huber, but follow Hoehne (1954) who considered it a synonym of *V. planifolia*. The material of *V. carinata* Rolfe is very inadequate, and we are not completely sure that it is conspecific with *V. planifolia*.

This species has several allies with which it can be confused, particularly *V. hartii*, *V. insignis*, *V. odorata* and *V. tahitiensis* (see comments under those species).

COLLECTIONS: MEXICO: *Pavón* (actually Sessé and Mociño) *s.n.* (G 7889/150!); *without collector* (G 7889/106!); *Schott s.n.* (BM!); *Comisión Geográfico-Exploradora 7725* (AMES!); *González in Oestlund 5790* (AMES!); *Nagel in Oestlund 5001* (AMES!); *Nagel in Oestlund 5050* (AMES!). GUATEMALA: *Lehmann 1436* (BM!); *Standley 25064* (AMES!); *Johnson 1178* (AMES!). BELIZE: *Gentle 2894* (K!); *Schipp S-971* (AMES!). HONDURAS: *Standley 55583* (AMES!); *Yuncker 4993* (AMES!). COSTA RICA: *Brenes 690* (F!); *von Wedel 1529* (BM!); *Standley & Valerio 48904* (AMES!). PANAMA: *Standley 29103* (AMES! sterile); *Standley 29731* (AMES! sterile); *Proctor 287* (AMES!). SOURCES: Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 234-239, fig. 108; Garay, L.A. 1978. *Flora of Ecuador. Orchidaceae I*: 49-52, fig. 15; Dodson, C.H. & P.M.. 1980. *Ic. Pl. Trop. pl.* 354; Hamer, F. 1984. *Ic. Pl. Trop. pl.* 1194; Dodson, C.H. & H.H. Gentry. 1985. *La Flora de Jauneche*: 110, pl. 44-B; Castillo Mayda, M. & J.D. Ackerman. 1992. *The Orchids of Puerto Rico and the Virgin Islands*: 54, pl. 11; Ackerman, J.D. 1995. *An Orchid Flora of Puerto Rico and the Virgin Islands*: 176, fig. 96.

V. planifolia var. *gigantea* Hoehne = *V. hostmanii*

V. planifolia var. *macrantha* Griseb. = *V. phaeantha*

SOURCES: Gloudon, A. & Tobisch, C. 1995. Orchids of Jamaica.: 207-208. Foldats, E. 1969. Flora de Venezuela. Orchidaceae I: 123, fig. 42 (this drawing may be based on a different species); Dodson, C.H. & Gentry, H.H. 1985. La Flora de Jauneche: 110, pl. 44-B.

79. *V. platyphylla* Schltr. in Repert. Sp. Nov. Regni Veg. 10: 7 (1911). Type: Sulawesi, Gunung Klabat, c. 400 m, 13 Dec. 1909, *Schlechter 20556* (holo. B†; iso. K!).

DISTRIBUTION: Endemic to Sulawesi.

This poorly known species has the vegetative aspect of *V. kinabaluensis*; the inflorescence, although truncate in the type, seems to be many-flowered. Also the large, thick capsule and the form of the buds are reminiscent of *V. kinabaluensis*. An illustration of a floral dissection is provided by Mansfeld (1934).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 213; Mansfeld, R. 1934. Repert. Sp. Nov. Regni Veg. 74: t. 14.

V. pleei Portères in Bull. Soc. Bot. France 58: 94 (1951). Type: Ile de la Martinique, *Plée 621* (holo. P).

Garay & Sweet (1974) suspected that this species was based on a mixed collection apparently containing the leaves of *V. mexicana* and the flowers of *V. pompona* or of an allied species.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 262; Garay, L.A. & H.R. Sweet. 1974. Flora of the Lesser Antilles. Orchidaceae: 46.

80. *V. poiteai* Rchb. f. in Linnaea 41: 66 (1877). Type: Santo Domingo, *Poiteau s.n.* (holo. W 19346!).

V. aphylla sensu Eggers in Vidensk. Meddel Dansk Naturhist. Foren. Kjoebenhavn 21 (1889), *non* Blume (1825). Type: Santo Domingo, Llanos de Rafael, 200 m, 7 June 1887, *Eggers 1958* (iso. K! sterile; G 7889/172! sterile).

V. eggersii Rolfe in J. Linn. Soc. Bot. 32: 472 (1896). Based on *V. aphylla* Eggers.

V. correllii Saulea & R.M. Adams in Brittonia 33(2): 192 (1981). Type: Bahama Islands, Grand Bahama, Freeport Hammock, off Coral Road, *Correll, Popenoe & Fluck 45441* (holo. NY; iso. FTG).

DISTRIBUTION: Bahamas, Cuba, Hispaniola, and Puerto Rico.

This is a “leafless” American *Vanilla*, in which small, hooked leaves are present at each node. It has a large flabellate lip with a recurved apical lobe and an irregular, crisped and maroon margin. The identity of this species has been recently solved by Ackerman (1995) who studied all the leafless Caribbean vanillas.

COLLECTIONS: DOMINICAN REPUBLIC: *Fuertes 912* (BM! K!); *Wright 3351* (BM! AMES!, K! sterile; formerly mixed with the isotype of *V. phaeantha*). PUERTO RICO: *Garber 20* (K! fruits only).

SOURCE: Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 169-171, fig. 92.

81. *V. polylepis* Summerh. in Bot. Mus. Leafl. 14: 219 (1951). Type: Northern Rhodesia (Zambia): Mwinilunga District, River Matonchi, 23-24 Oct. 1937, *Milne-Redhead 2930* (holo. K!; iso. K!).

V. schliebenii Mansf. ex Schlieben in Gartenflora, 1937: 86: 42, 43, 58 (1937), *nomen*. Based on: Tanzania, *Schlieben 1422* (G!; Z!).

DISTRIBUTION: Kenya, Tanzania, Zambia, Malawi, Democratic Republic of the Congo, Zimbabwe, Angola, Uganda.

A species closely related to *V. imperialis*, differing by its notched lip, shorter, broader tepals, lip with several rows of transverse, branching scales (not fine hairs), and a purple-violet blotch on lip, rather than a lip marked with streaks.

COLLECTIONS: D.R. CONGO: *Seighita 3570* (BR, K!); *Rogers 148* (BM! K!); *van Hirschberg 28* (K!). KENYA: *Verdcourt 1011* (K!); *Piers 75* (K!, drawing),[‡] *19527* (K!). TANZANIA: *Burt 18136* (BM!); *Petterson 3-a* (K!). ZAMBIA: *Milne-Redhead 4265* (K!); *Richards 2026, 15355, 20509* (K!); *Morze 126A, 126B* (K!); *Bredo in Moreau 864, 864A, 864B, 867* (K!); *Fanshawe 2545* (K!),[‡] *9660* (K!); *Stevenson 1653* (K!); *Holmes 0137* (K!); *Burt 6338* (K!); *Harder et al. 2044* (K!). MALAWI: *La Croix et al. 880* (K!); *Pawek 1020* (K!). ZIMBAWE: *Ball 844* (K!); *Chase s.n., 3896* (K! BM!),[‡] *4307* (K! BM!),[‡] *4680* (K!, pictures; BM!); *Renz et al. 11344* (K!); *Flowers 2667* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 202-203; Stewart, J. & Campbell. 1970. Orch. Trop. Afr.: 114, t. 45; Hunt, P.F., 1974. K.B. 29:

425; Stewart, J. 1974. Upland Kenya Wild Flowers: 756; Williamson, G. 1977. Orchids of South Central Africa: 146, fig. 78, t. 124; Cribb, P. 1984. Flora of Tropical East Africa. Orchidaceae 2: 261, fig. 51; Geerinck, D. 1984. Flore D'Afrique Centrale (Zaire, Rwanda-Burundi): 243-244; Stewart, J. 1996. Orchids of Kenya: 89-90; Szlachetko, D.L. & S. Olszewski. 1999. Fl. de Cameroun: 288, pl. 102, I-M.

82. *V. pompona* Schiede in Linnaea 4: 573 (1829). Type: Mexico, *Schiede 1043* (lecto. BM!, designated by Garay, Fl. Ecuador Orch. 1:52. 1978; isolecto. K! LE! P! W!).

V. pittieri Schltr. in Repert. Spec. Nov. Regni Veg. 3: 106 (1906). Type: Costa Rica, *Pittier 6600* (holo. B†; trace at AMES 24329!).

DISTRIBUTION: Mexico, Nicaragua, Costa Rica, and probably W Colombia and Ecuador.

Vanilla pompona is a variable, widely distributed species. We consider it to be a species complex. The specific name is based on a Mexican specimen collected in central Veracruz. Mexican populations are apparently isolated from the rest of the populations of the species because there are no known populations in Chiapas, Guatemala, Belize, or El Salvador. It reappears only in Central Honduras and Nicaragua.

COLLECTIONS: MEXICO: without precise locality, *Sallé* (BM!). Michoacan, *Hinton et al. 13815* (AMES!); *15910* (AMES!). Guerrero, *Langlassé 941* (AMES! G 7889/153! 154! K!); *Hinton 11387* (K!). OAXACA: *Cuming s.n.* (G 78889/155!); *Nagel in Oestlund 4574* (AMES!); Copalita, *Nagel & González in Oestlund 6102* (AMES!); Veracruz, *Bourgeau 2232* (K!); *Nagel in Oestlund 2684* (AMES!). COSTA RICA: *Alfaro 269* (AMES!). COLOMBIA: *Smith 2370* (K!) & *2371* (AMES! K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 223-226, fig. 102 and 234 (as *V. pittieri*); Garay, L.A. 1978. Flora of Ecuador. Orchidaceae I: 52, fig. 16; Hamer, F. 1984. Ic. Pl. Trop. t. 1195; McVaugh, R. 1985. Flora Novo-Galiciana 16: Orchidaceae: 351-353, fig. 115; Ackerman, J.D. 1995. An Orchid Flora of Puerto Rico and the Virgin Islands: 174-176; Pupulin, F. 1998. Orchid Florula of Parque Nacional Manuel Antonio, Quepos, Costa Rica. Rev. Biol. Trop. 46(4): 1029.

V. ponapensis Kaneh. & K.Yaman. = *Pseudovanilla ponapensis* (Kaneh. & K.Yamam.) Garay.

V. porteresiana Veyret & Szlach. = *V. hostmanii*

V. preussii Kraenzl. = *V. inodora*

83. *V. pseudopompona* Soto Arenas, ined.

DISTRIBUTION: Panama.

This species is very near to *V. pompona*, but it has smaller, narrower leaves, and flowers with a much larger penicillate callus.

COLLECTIONS: PANAMA: *Seeman 1159* (BM! K-L!); *Allen 4428* (G 7889/121!); *Hunter & Allen 852* (AMES! G7889/151!); *Powell 137* (AMES! BM!); *Powell 3507* (AMES!); *Maxon 6779* (AMES!); *Standley 29919* (AMES!); *Bangham 458* (AMES!); *Piper s.n.* (AMES!).

V. pterosperma Wall. ex Lindl. = *Galeola hydra*

V. purusara Barb. Rodr. ex Hoehne = *V. appendiculata*

84. *V. ramificans* (J.J. Sm.) J.J.Sm. in Bull. Jard. Bot. Buitenzorg ser. 3, 2: 22 (1920). Based on same type as *V. ramosa* J.J.Sm.

V. ramosa J.J.Sm. in Repert. Sp. Nov. Regni Veg. 11: 130 (1912), non Rolfe. Type: New Guinea, Papua (Dutch New Guinea), Jayapura (Hollandia), *Gjellerup 706* (holo. L).

DISTRIBUTION: New Guinea: Irian Jaya and Papua New Guinea, in the Southern Highlands Province and on Normanby Island.

The small leaves (100-130 × 25-40 mm) and the branched inflorescence are characteristic among the New Guinean species. The cream and red flowers and the many-flowered inflorescence suggest a relationship with the *V. kinabaluensis* complex. We have examined specimens cultivated in the National Botanic Gardens, Papua New Guinea which correspond well with the published drawings and share with other New Guinean species the very thick ovaries

COLLECTION: PAPUA NEW GUINEA: *Lelean & Streimann LAE 52525* (K!).

SOURCES: Smith, J.J. 1915. Die Orchideen von Niederländisch-Neu-Guinea: 187, t. 62, 100; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 210; Howcroft, N.H.S. 1984. A Guide to the monocotyledons of Papua New Guinea. R.J. Johns

& Hay, A.J.M. (eds.) 4. The Orchidaceae (in part): Forestry Department PNG, University of Technology. p. 126, fig. 74; O'Byrne, P. 1994. Lowland Orchids of Papua New Guinea. SNP Ltd. p. 9.

85. *V. ramosa* Rolfe in J. Linn. Soc. Bot. 32: 457 (1896). Types: West Tropical Africa, Niger, about Angiama, *Barter 20134* (lecto. K! selected by Geerinck, 1984); interior of Western Lagos, *Rowland s.n.* (syn. K!).

V. ovalifolia Rolfe in J. Linn. Soc. Bot. 32: 457 (1896). Type: West Tropical Africa, Old Calabar, *Thomson 132* (holo. K!).

V. laurentiana De Wild, Not. Pl. Utiles Congo, 1: 327 (1903). Type: Zaire, Nala, 1903, *van Rysselberghe 5* (holo. BR, iso. K!).

V. africana Lindl. var. *laurentiana* (De Wild.) Portères in Bull. Soc. Bot. France 98: 126 (1951).

V. laurentiana De Wild. var. *gilletii* De Wild., loc. cit. 325 (1951). Type: Zaire: between Kisatu and Kimpassa, *Collet 3362* (holo. BR; iso. K!).

V. africana Lindl. subsp. *ramosa* (Rolfe-Szlach. & Olszewski in Fl. Cameroun 34: 286 (1988).

DISTRIBUTION: Ghana, Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo, Democratic Republic of the Congo and Central African Republic. The reports from Eastern Africa are here considered as *V. zanzibarica*.

Vanilla ramosa is a member of the *V. africana* complex in which the inflorescences are usually branched, the oblong-elliptic leaves are much broader, and the midlobe of the lip is oblong-elliptic and apiculate-acuminate. In living condition the lip is rather flat, rather than conduplicate-gibbose as in *V. crenulata* which also has large, broad lower bracts in the simple raceme. Some authors (e.g. Geerinck, 1984) have treated *V. ramosa* as synonym of *V. crenulata*, but it differs in the conduplicate-gibbose lip of *V. crenulata*, in its broadly elliptic to suborbicular lower bracts of the inflorescence and in its larger lip measurements.

COLLECTIONS: GHANA: *Bowling 36647* (K!); *Irvine 2197* (K!); *Andoh FH 5257* (K!). NIGERIA: *Talbot s.n.* (K!); *Kennedy 220, 2081* (K!). CAMEROON: *Bates 1117* (BM!); *Zenker 1127* (BM! K!) & 3010a (BM! K!); *Thomas 5922* (K!); *Binuyo & Daramola FHI 35648* (K!); *Leeuwenberg 5465* (K!). GABON: *Le Testu 863* (BM!), *7723* (BM! K!), *9015* (BM! K!);

Tisserant 1575 (BM!). D.R. CONGO: *De Giorgi 1715* (AMES! BM! K!); *Louis 8577* (BM!); *Vermoesen 1869* (K!); *Lebrun 1948* (K!); *Germain 4520* (K!); *Lebrun 2493* (K!). EQUATORIAL GUINEA: *Tessmann 224* (K!). WITHOUT LOCALITY: *Kew spirit collection 45787* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 198-200, fig. 93; Geerinck. 1984. Flore D'Afrique Centrale (Zaire, Rwanda-Burundi): 239-242; Summerhayes, V.S. 1968. Flora of West Tropical Africa 3(1): Orchidaceae: 205-206; Szlachetko, D.L. & S. Olszewski. 1988. Fl. Cameroun 34: 286.

V. ramosa J.J. Sm. = *V. ramificans*

86. *V. ribeiroi* Hoehne, Comm. Lin. Telegr., Bot. 1: 28 (1910). Type: Brazil, Matto Grosso, by Rio Jaurú, near Praxedes, Nov. 1908, *Ribeiro in Hoehne 997* (holo. RJ 2512!).

DISTRIBUTION: Brazil, Guyana, and Amazonian Colombia.

This species has white flowers and a lip adorned with conspicuous apical, retrorse, yellow trichomes. The lip covered with hairs is reminiscent of that of the Central American *V. helleri*, which has a more trilobed lip and broader leaves; in *V. ribeiroi* the leaves are very short and narrow.

COLLECTIONS: COLOMBIA: *Schultes & Cabrera 15961* (AMES!). GUYANA: *Jansen-Jacobs et al. 2524* (K!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 185-186

V. ronoensis Hayata = *V. somai*

87. *V. roscheri* Rchb. f. in Linnaea 41: 65 (1877). Type: Tanzania, Zanzibar, 1851, *Roscher s.n.* (holo. W 19388! W 19389! drawings; K! tracing of W specimen).

DISTRIBUTION: Ethiopia, Kenya, Somalia, Tanzania (including Zanzibar and Pemba), Mozambique, South Africa.

This leafless vanilla has spectacular white flowers with an apricot or pale pink throat to the lip, petals which are very broad and a lip with a somewhat undulate margin. It is very closely related to *V. madagascariensis* and *V. phalaenopsis* from the Seychelles; if they are considered conspecific, the

correct name for the species is *V. phalaenopsis*, the oldest epithet.

Vanilla roscheri is common in tropical deciduous coastal forests of Kenya and Tanzania, and it is occasionally cultivated as ornamental. It has been only recently recorded from near Lake Sibaya in South Africa.

COLLECTIONS: KENYA: *Bally 8144* (K! K photos!), *B10462* (G 7889! K!), *8540* (K!); *Verdcourt 1195, 3223* (both K!); *Brenan et al. 14549* (K!); *Faden & Evans 70/781* (K!); *Polhill & Paulo 876, 972* (K!); *Napper 1468* (K!); *Tweedie 1217* (K!), *1260* (K!); *Drummond & Hemsley 4118* (K!); *Graham 1605* (K!); *Greenway s.n.* (K!), *9487* (K!); *Perdue & Kibwa 10125* (K!). TANZANIA: *Greenway & Turner s.n.* (K photo!); *Greenway 12455* (K!), *Moreau 134* (K!); *134A* (K!); *Archbold 2786* (K!); *Richards 21992* (K!); *Franzier 1185* (K!); *Vaughan 2530, 2703, 2785* (all K!); *Greenway 4125* (K!); *Tanner 2453* (K!); *Cribb & Grey-Wilson 10013* (K!); *Mwasumbi & Khero 11000* (K!); *Curle 442* (BM!); *Pemba, Lambu s.n.* (K!); *Vaughan 937* (K!); *Zanzibar, Kirk 3/701* (K!), *3/78* K! drawing); *Lyne 4* (K!); *Greenway 1315* (K!), *2669* (K!); *Wigg s.n.* (K!); *Burt 2626, 2628* (K!); *Vaughan 45* (BM!), *1662, 2153, 2173* (all K!). SOUTH AFRICA: *C.J. & M.C. Ward 59* (K! NH), *338* (K!). MOZAMBIQUE: *Janson 7492* (K!); *Danitree s.n.* (K!); *de Koning & Hiemstre 8990* (K!); *Ball 934* (K!); *Gómez & Sousa 4908* (K!); *Grandvaux B 7724* (K!); *Ball 1000* (K!); *Watmough 351* (K!); *Greenamdijk & de Koning 316* (K!); *W.E. Taylor s.n.* (BM!); *Scott Elliot 6132* (BM!).

SOURCES: Rolfe, R.A. 1897. *Fl. Trop. Afr.* 7: 179; Piers, F. 1959. *Orch. E. Afr.*: 50 & 1968. ed. 2: 82, fig. 29; Tweedie, E.M. 1964. *J. E. Afr. Nat. Hist. Soc.* 24: 41; Cribb, P. 1984. *Flora of Tropical East Africa. Orchidaceae* 2: 258-259, fig. 260; Stewart, J. 1996. *Orchids of Kenya*: 90; Linder, H.P. & H. Kurzweil. 1999. *Orchids of Southern Africa*: 350-351.

V. rubiginosa Griff. = ?*Galeola hydra*

V. rubra (Lam.) Urb. = ?*V. planifolia*

88. *V. ruiziana* Klotzsch in *Bot. Zeitung* (Berlin) 4: 563 (1846). Type: Peru, Chicoplaya, *Ruiz & Pavón* (holo. B †; iso. AMES 38626! and photo, G 7889/ 167! F!; tracing K! BM! G 158!).

V. weberbaueriana Kraenzl. in *Bot. Jahrb. Syst.*

37: 395 (1906). Type: Peru, Prov. Tarma, Dep. Junin, near la Merced, Chanchamayotal, 1000 m, *M. Weberbauer 1849 (?18348)* (holo. B †, AMES 38631 photo! iso. MOL!).

DISTRIBUTION: Peru and Bolivia.

The identity of *V. ruiziana* has remained obscure since its publication in 1846. The holotype specimen, lost when the Berlin Herbarium was destroyed, was sterile, having stout stems and acute to acuminate, lanceolate-oblong leaves. However, at least a duplicate of the same collection (“247 *Epidendrum lanceolatum*, *vaynilla vulgo*, *folium cum caule*, *et flor*” in *Ruiz & Pavón* manuscript, and annotated “M. Pavón”, perhaps in *Reichenbach’s* hand) has been found in Geneva (G 7889/167)! The flowers are relatively poorly preserved, but it is possible to appreciate its granulose sepals and ovary surface, the thickened veins of the lip and the acute, strongly subcalyprate sepals. This combination of characters is exclusive to the modern specimens from Peru and Bolivia. The type specimen of *V. weberbaueriana*, although bearing only young buds, also belongs here.

Leaf shape differences between the types of *V. ruiziana* and *V. weberbaueriana* seem striking, but there are intermediate specimens connecting both extremes. The vegetative parts of *V. ruiziana* seem to be taken from a shaded spot.

Portères (1954) assigned *V. weberbaueriana* to subsection *Membranacea* (= subsect. *Vanilla*). The study of more abundant material shows that *V. ruiziana* is closely related to *V. hostmanii*, differing mostly in its shorter inflorescences, the tepals which are acute, the sepals conspicuously calyprate and a larger, ovate midlobe to the lip which bears 1-3 elevated, axial keels near the apex.

COLLECTIONS: BOLIVIA: *White 2326* (AMES!). PERU: *Killip & Smith 27430* (AMES!); *Rubio Kayap 223* (MO 2922173!).

SOURCES: Portères, R. 1954. *Le Genre Vanilla et ses Espèces*: 233 and 253-254; Schweinfurth, C. 1958. *Orchids of Peru I. Fieldiana: Botany* 30: 44.

V. sativa Schiede = *V. planifolia*

89. *V. savannarum* Britt. in *Mem. Torr. Bot. Club* 16: 61 (1920). Type: Cuba, near Camagüey, *Britton & Cowell 13210* (not seen)

DISTRIBUTION: Cuba.

Well-preserved flowers of this species are unknown to us. However, old flowers and dissected buds show a very close relationship with the South American *V. palmarum*, and these species must be compared carefully to determine if they are distinct. With *Vanilla palmarum*, it shares the similar habit and habitat, the lack of a penicillate callus, the presence of 5-6 axial, shortly pubescent lines on the distal half of the lip, the long lanuginose area beneath the stigma, and the lip fused to the column for only about a half of the column length. The densely-fruited raceme and the pods with a well-developed calyculus are also similar. The many fruits per inflorescence suggest self-pollination.

COLLECTIONS: CUBA: *González 288* (AMES!); *Clemente & Alain 1050* (AMES!); *Schaffer 615* (para. AMES!), & *1072* (para. AMES! K!); *Ekman 19043*.

SOURCES: Acuña, G.J. 1939. Catálogo Descriptivo de las Orquídeas Cubanas: 21-22; León, F.S.C. & F.S.C. Alain. 1946. Flora de Cuba 1: 352, fig. 147.

V. schliebenii Summerh. = *V. polylepis*

90. *V. schwackeana* Hoehne in Arq. Bot. Estado São Paulo 1: 125. t. 135 (1944). Type: Brazil, Minas Gerais, *Schwacke 11106* (holo. RJ 37015!).

This species seems to be related to *V. cristagalli*, but the ornamentation on the lip is much reduced to warty, apical papillae. Hoehne (1944) indicated that the specimen could be a mixture of parts of different species, the leaves being very long acuminate, and thin. Specimens collected in Amazonia (*J.B.F. da Silva 590*, MG!) have flowers indistinguishable from those of the type of *V. schwackeana*, but with thick, coriaceous, oblong-elliptic leaves with recurved margins, suggesting that Hoehne's doubts about the mixture nature of the type specimen had substance.

COLLECTIONS: BRAZIL: PARA: *da Silva 590* (MG!), *591* (AMO! sterile).

91. *V. seranica* J.J. Sm. in Bull. Jard. Bot. Buitenzorg ser. 3, 10: 93 (1928). Types: Moluccas, Ceram, *Rutten 1800 & 1880* (syn. L).

DISTRIBUTION: E Indonesia, Moluccas.

Said to be allied to *V. abundiflora* and *V. klabatensis*.

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 215.

92. *V. seretii* De Wild. in Bull. Jard. Bot. État 5(2): 180 (1916). Types: Zaire, near Nala, 1907, *Seret 756* (syn. BR); near Arebi, 1906, *Seret 714*; Nala (syn. BR); 1911, *Boone III* (syn. BR); Libenge, 1913, *Mestdagh 59* (syn. BR; isosyn. BM!).

V. tisserantii Portères in Bull. Soc. Bot. France 98: 93 (1951). Type: Central African Republic (French Equatorial Africa), Bukoko, Oubangui, SW of Bangui, 18 Aug. 1947, *Tisserant 151* (holo. P; iso. BM! G!).

DISTRIBUTION: Democratic Republic of the Congo and Central African Republic.

This is another member of the *V. chalongii* group, in which the lip is deeply saccate. It is distinguished from *V. nigerica* by its lip in which the throat has few hairs and lacks a gibbous base.

COLLECTION: D.R. Congo: *H. Callens 906* (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 172-174, fig. 83 (as *V. tisserantii*); Szlachetko, D.L. & S. Olszewski. 1999. Fl. de Cameroun: 288, t. 102, A-H.

Vanilla shenzhenica Z.J. Liu & S.C. Chen = *V. somai*

93. *V. siamensis* Rolfe ex Downie in Bull. Misc. Inf. Kew 1925(10): 410-411 (1925). Type: Thailand, Doi Sutep, 690 m, *Kerr 95* (holo. K!; iso. C!).

V. pierrei Gagnep. in Bull. Mus. Hist. Nat. (Paris) 3: 686 (1931). Types: Cambodia, Mts Kamchay, Prov. Kampot, *Pierre 1560* (syn. P); Cambodia (Cochinchina), Mts Binh-dinh, *Pierre s.n.* (syn. P).

DISTRIBUTION: Thailand, Kampuchea (Cambodia), Vietnam, China (Yunnan).

This species is characterized by its large, broadly elliptic or ovate, shortly apiculate leaves. The large flowers have very long, flat papillae at the lip apex. It is similar to *V. abundiflora* and *V. kinabaluensis*.

We here consider *V. pierrei* to be conspecific. It was described from immature buds, but the general appearance is the same as *V. siamensis*. However, we would like to compare better material of *V. pierrei* with that of *V. siamensis*. *Vanilla siamensis* is a montane species found from 700 to 1300 m elevation.

COLLECTIONS: THAILAND: *R. Geesink et al. 6755* (K!), *6698* (K!); *without collector 38* (K! sterile).

SOURCES: Gagnepain, F. & A. Guillaumin. 1932. Flore Générale de L'Indo-Chine 2. Orchidacées: 582-584, fig. 55 10-13; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 210-212, fig. 98 and 218-219, fig. 101 (as *V. pierrei*); Seidenfaden, G. & T. Smitinand. 1959. The Orchids of Thailand: a preliminary list, part 1: 60, fig. 41; Averyanov, L. 1988. Predvaritelnyy spisok orkhidnykh: 112 (as *V. pierrei*); Averyanov, L.V. 1994. Identification Guide to Vietnamese Orchids: 76 (as *V. siamensis*); Chen, S., Z. Tsi & Y. Luo. 1999. Native Orchids of China. Science Press, Beijing: 411.

94. *V. somai* Hayata, Ic. Pl. Formosan. 6: 88, t. 14 (1916). Type: TAIWAN, between Urai and Agisku, May 1916, *Hayata s.n.* (holo. TI).

Vanilla griffithii sensu Hayata in J. Coll. Sci. Imp. Univ. Tokyo 30, 1: 343 (1911), *non* Rchb. f. (1854).

Vanilla griffithii Rchb. f. var. *formosana* Ito, Icon. Pl. Japan. 1(4): 1 t. 1 (1911).

Vanilla ronoensis Hayata, Icon. Pl. Formosan. 9: 114 (1920). Type: Taiwan, between Rono and Kosenpo, April 1917, *Hayata s.n.* (holo. TI).

Vanilla griffithii Rchb. f. var. *ronoensis* (Hayata) S.S. Ying, Col. Illustr. Indig. Orch. Taiwan; 1(2): 509 (1977).

Vanilla albida sensu H. J. Su in Huang, T.S. et al. (eds), Flora of Taiwan 5: 1065 (2000), *non* Blume (1823).

Vanilla shenzhenica Z.J. Liu & S.C. Chen in Acta Phytotax. Sinica 45, 3: 301 (2007). Type: China, Guangdong, Shenzhen, Longgang, Meishajian, 22 Feb 2005, *Liu* 3025 (holo. NOCC).

DISTRIBUTION: Taiwan, Vietnam, and China.

The rather small flowers with a short tube, the high, flattened papillae arranged in two rows at the lip apex, and the inflorescences with two flowers open simultaneously are characteristic. Its inflorescence structure is similar to that of *V. annamica*, but in that species the inflorescence is much branched, and the flowers less than half the size.

COLLECTIONS: CHINA: Guangdong, *Liu* 3025 (NOCC!). TAIWAN: *Price* 302 (K!), 302 bis (K!); *Henry* 479 (K!).

SOURCES: Hayata, B. 1911. J. Col. Sci. Univ. Tokyo 30(1): 342 (as *V. griffithii*); Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 183 (as *V. ronoensis*) and 184-

185, fig. 87; Su, H.J. 1985. Native Orchids of Taiwan. pl. 50: 54-1 (as *V. griffithii*); Ying, S.S. 1977. Coloured Illustrations of Indigenous Orchids of Taiwan 1: 338-340, pl. 339 (as *V. griffithii* var. *formosana*); Chow Cheng. 1989. Formosan Orchids. Epiphytes: 204-206 (as *V. albida*); Tsan-Piao Lin. 1975. Native Orchids of Taiwan: 248-249.

V. speciosa Boxall ex Neves, in Blanco, Fl. Philipp. de. III. Nov. App. 248, *nomen*.

95. *V. sprucei* Rolfe in J. Linn. Soc. Bot. 32: 461 (1896). Type: Colombia, R. Vaupés, Nov. 1852, *Spruce* 2727 (holo. K-LINDL!).

DISTRIBUTION: Amazonian Colombia.

This species is rather mesophytic, the type having slender stems, drying almost black, and thin leaves covered with epiphylls. The parallel veins and transverse secondary veins of the leaves resemble those of *Epistephium* leaves. The raceme is lax with about 4 to 8 (perhaps more) successive whitish-green flowers with very narrow tepals and a very long tubular lip with a conspicuous penicillate callus. The flowers seem to develop over a long period, and small, undeveloped buds are present when one flower is in anthesis, perhaps in the way described for *V. pauciflora*, to which might be related. *Schultes & Cabrera* 12497 has inflorescences branched at base, very odd for American species. A calyculus is scarcely present.

COLLECTION: COLOMBIA: *Schultes & Cabrera* 12497 (AMES!).

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 247.

96. *V. sumatrana* J.J. Sm. in Bull. Jard. Bot. Buitenzorg, ser. 3, 2: 22 (1920). Type: SUMATRA, Benkoelen, Bukit Barisan, Rimbo-Pengadang, 1000 m, June 1916, *Jacobson & Ajaeb* 210 (L not seen).

DISTRIBUTION: Sumatra.

A little known species which, in the protologue, was compared with *V. griffithii* Rchb. f., but differs in the narrowly spatulate sepals and petals, the small shortly bilobed but not flabellate midlobe of the lip, the series of transverse lamellae beneath the hair cushion, and the different anther. It has a reddish lip. It is found at higher elevations, more than 1000 m, than *V. griffithii*.

SOURCES: Carr, C.E. 1935. Two Collections of Orchids from British North Borneo 1. Gard. Bull. Straits Settlements: 8: 176; Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 216-218, fig. 100.

V. surinamensis Rehb. f. = *V. guianensis*

97. *V. tahitiensis* J.W. Moore in Bull. Bernice P. Bishop Mus. 102: 25 (1933). Type: Society Islands, Raiatea, Moore 294 (holo. BISH!).

V. tiarei Costantin & Bois in Compt. Rend. 161: 201 (1915), *nomen nudum*.

V. hirsuta M.A. Clem. & D.L. Jones in Lasianthera 1(1): 47 (1996). Type: Papua New Guinea, Clements 6742 (holo. CANB; iso. NCBG).

V. tahitiensis var. *haapape* Portères, Bull. Soc. Bot. France 98:127 (1951), *nomen nudum*. Based upon: cult.. Tahiti, without further provenance.

V. tahitiensis var. *potiti* Portères, Bull. Soc. Bot. France 98: 127 (1951), *nomen nudum*. Type: cult. Tahiti, 1926, without further provenance.

Vanilla tahitiensis is the second most important vanilla for production of aromatic pods. It is closely related to *V. planifolia* and *V. odorata* and a member of the American clade of the genus with penicillate callus. Its distribution in the South Pacific Islands is striking, and it is very probable that it is a hybrid distributed originally from the Philippines and taken to its present area by man. A good drawing of it is provided by Howcroft (1984). The Tahitian vanilla is a probably a hybrid between *Vanilla odorata* and *V. planifolia*. Five varieties are listed by Portères (1959). COLLECTIONS: FRENCH POLYNESIA: Raiatea, *St. John* 17310 (K!); Mongareva Isl., *St. John* 14459 (K drawing!).

SOURCES: Howcroft, N.H.S. 1984. A Guide to the monocotyledons of Papua New Guinea. R.J. Johns & A.J.M. Hay (eds.) 4. The Orchidaceae (in part): Forestry Department PNG, University of Technology: 129, fig. 71. Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 239-242, fig. 109.

Vanilla taiwaniana S.S. Ying. See in excluded species.

Vanilla tiarei Costantin & Bois = *V. tahitiensis*

V. tisserantii Portères = *V. seretii*

V. tolepephora Ridl. = ?*V. griffithii*

98. *V. trigonocarpa* Hoehne in Arq. Bot. Estado São Paulo, n.s., 1(6): 126 (1944). Type: Brazil, Pará, outskirts of Belem do Pará, 23 Nov. 1926, *Ducke s.n.* (holo. RJ 19445!).

V. pauciflora R.L. Dressler in Orquideología 13(3): 229 (1979). Type: Panama, *Dressler* 5290 (holo. US).

DISTRIBUTION: Costa Rica, Panama, Colombia and Brazil.

A very distinct *Vanilla* known from wet forests in Central America, Colombia, and from the delta of the Amazon River. The main difference between *V. trigonocarpa* and *V. pauciflora* is the more trilobed lip of *V. trigonocarpa*. The plant seems to be related to *V. espondae* from Colombia, and perhaps to *V. sprucei*.

COLLECTION: COSTA RICA: *Catling & Brownell* C24.1 (AMES!).

99. *V. utteridgei* J.J. Wood in Orchid Rev. 110: 232 (2002). Type: New Guinea, Papua, Mimika Regency, Kuala Kencana, *Utteridge* 456 (holo. K).

DISTRIBUTION. New Guinea: S Papua only.

Closely allied to *V. kempteriana*, differing in its pubescent column and the two lateral calli in front of the penicillate callus.

V. uncinata Huber & Hoehne = *V. odorata*

V. vanilla (L.) H. Karst. = ?*V. mexicana*

V. vanilla (L.) Huth = ?*V. mexicana*

100 *V. vellozii* Rolfe in J. Linn. Soc. Bot. 32: 467 (1896). Type: Brazil, *Glaziou* 14302 (lecto. K! designated here).

V. chamissois var. *brevifolia* Cogn., Fl. Bras. 3(4): 149 (1893). Based on *Epidendrum vanilla* Vellozo, F.Flum. Ic. 9: t. 1 (1827).

V. argentina Hicken in Anales Soc. Ci. Argent: 235. 1916; *Vanilla* Argent. 3 (1917). Types: Argentina, Formosa, Pilcomayo, *Cáceres* (not seen; 3 immature fruits only); Gran Chaco, *J. Domínguez* 307, 25-IX-1915, Inst. Darwiniano

DISTRIBUTION: Brazil, Paraguay, Argentina.

This species has been confused with *V. chamissonis* but it is easily distinguished by its shorter segments, especially its very broad, subentire lip. *V. chamissonis* has a very elongate midlobe to the lip

and longer tepals. It seems to be common in coastal areas. However, they are probably closely related, sharing with *V. calyculata* the conspicuous calyculus, especially on ovaries whose flowers have just faded.

COLLECTIONS: BRAZIL: Parana, *Dusén 16125* (AMES!). Rio de Janeiro, *Glaziou 11621* (K! without flowers). Sao Paulo, *van der Berg s.n.* (AMO slides!). PARAGUAY: *Fiebrig 564* (K! AMES! G7 889/113!).

101. *V. verrucosa* Hauman in An. Mus. Nac. Buenos Aires 29: 365-366 (1917). Type: ARGENTINA, Misiones, Piray, March 1901, *Kermes 127* (holo. Herb. Min. Agr. 6358; not seen)

V. verrucosa is distinguished from its close relatives by its very small dimensions and the triangular acuminate midlobe of the lip. Andrés Johnson (pers. com.) indicates that the type specimen is sterile and that the species has not been recollected. He stated that is not improbable that *V. verrucosa* is an atypical form of *V. rojasiana* Hoehne (= *V. angustipetala* Schltr.). We suspect that the original description might have been based on an immature bud.

The small members of the membranaceous group found in Brazil and Argentina are a taxonomically difficult complex, due to the scarcity of material, poor preservation or condition of the type specimens, and the similarity of the described taxa.

Vanilla angustipetala (syn. *V. rojasiana*) and *V. parvifolia* have almost identical habits, inflorescences and flowers, except for the presence of lamellae in *V. parvifolia* and rows of warts on the lip in *V. angustipetala*. The plant illustrated in t. 22 of Hoehne's *Flora Brasílica*, and identified as *V. parvifolia*, shows longer, more acute leaves, longer inflorescences with more flowers and more acuminate sepals and narrow midlobe of the lip, approaching to *V. edwallii* or *V. organensis*.

SOURCE: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 188.

V. viridiflora Blume = *V. planifolia*

102. *V. walkeriae* Wight, Icon. Pl. Ind. Orient. t. 932 (1845). Type: SRI LANKA, *Walker s.n.* (holo. K!).

DISTRIBUTION: India and Sri-Lanka.

This species has been repeatedly confused with the other Indian leafless species such as *V. wightii*. *V. walkeriae* is similar to the Indian Ocean leafless

species *V. phalaenopsis* and *V. madagascariensis*, with large, white flowers bearing very broad petals and 2 longitudinal rows of hairs on the lip disc. It has been confused with *V. wightii*. Part of the confusion can be traced to a mixture of both leafless Sri Lankan species on the type sheet of *V. walkeriae* at Kew.

COLLECTIONS: SRI LANKA: *Champion s.n.* (K-LINDL!); *Diraviam & Anthony RHT 27780* (K!); *Mueller-Dombois et al. s.n.* (K!) & *69042619* (K!); *Thwaites s.n.* (K!) & *2964* (K!); *Cramer 4664* (K!). INDIA: *Fisher 1011a* (K!); *Wight s.n.* (K!).

SOURCES: Trimen, H. 1898. Handb. Fl. Ceylon 4: 220; Seidenfaden, G. 1983. The Flora of the Tamilnadu Carnatic. Orchidaceae: 1570-1571, pls. 698 and 699; Pradhan, U.C. 1976. Indian Orchids: Guide to Identification and Culture 1: 151; Jayaweera, D.M.A. 1981. Orchidaceae. A Revised Handbook to the Flora of Ceylon 2: 331.

103. *V. wariensis* Schltr. in Repert. Sp. Nov. Regni Veg. Beih. 1: 30 (1911). Type: PAPUA NEW GUINEA, *Schlechter 19928* (holo. B†).

DISTRIBUTION: Endemic to Papua New Guinea.

O'Byrne (1994) mentioned that it is common to the North of the Owen Stanley Range. It can be distinguished from other New Guinean vanillas by its very large leaves 27-35 × 5-7 cm.

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 212; Howcroft, N.H.S. 1984. A Guide to the monocotyledons of Papua New Guinea. R.J. Johns & Hay, A.J.M. (eds.) 4. The Orchidaceae (in part): Forestry Department PNG, University of Technology. p. 126; O'Byrne, P. 1994. Lowland Orchids of Papua New Guinea. SNP Ltd. p. 9.

V. weberbaueriana = *V. ruiziana*

104. *V. wightii* Lindl. ex White, Icon. Pl. Ind. Orient. sub t. 931 (1844). Type: S INDIA, *Wight 2091* (holo. K-LINDL! iso. K!).

V. aphylla Wight., Icon. Pl. Ind. Orient. t. 931 (1845), non Blume (1825). Based upon Travancore, Trevandrum, *Wight s.n.* (K).

V. wightiana Lindl. in Hook.f., Fl. Brit. India 6: 90 (1890), sphalm. pro *V. wightii*.

DISTRIBUTION: India (Deccan) and Sri Lanka.

This species has been confused in the literature. The type collections at K consist of different, separated

fragments on three sheets, some fragments seem to be referable to Wight's concept of *V. wightii*, and others to *V. walkeriae*. *Vanilla wightii* is closely related to *V. aphylla* and *V. calopogon*, while *V. walkeriae* is a member of the *V. madagascariensis* group. In *V. wightii* the inflorescences are short, with about 3 flowers, the lip has two rows of hairs from the base to the sides of the crest, which is like a large penicillate callus continuous with an apical strip of hairs. A fragment in each one of the isotypes at K shows an elongate inflorescence, with a thick fruit and many protuberant scars, lacking bracts, typical of *V. walkeriae*, in which the bracts are deciduous. Seidenfaden (1983) illustrated a specimen of *V. walkeriae* with narrow segments, but lacking the hirsute lip apex characteristic of the *V. aphylla* complex. Pradhan (1976) also illustrated *V. walkeriae* rather than the true *V. wightii*. A good illustration of *V. wightii* can be found in Abraham and Vatsala (1981). Although both species are leafless, *V. wightii* and *V. walkeriae* belong to different lineages of the genus.

Vanilla walkeriae resembles closely *V. roscheri* and its close allies, in having large, white flowers.

COLLECTIONS: WITHOUT LOCALITY: *cult. Hort. Bot. Reg. Kew a. 191* (K!, in part). SRI LANKA: *C. V. 2964* (K! watercolor).

SOURCES: Abraham, A. & Vatsala, P. 1981. Introduction to Orchids: 500-502. Seidenfaden, G. 1983. The Flora of the Tamilnadu Carnatic. Orchidaceae: 1570, pl. 698; Pradhan, U.C. 1976. Indian Orchids: Guide to identification and Culture 1: 151.

V. wrightii Rchb. f. = *V. bicolor*

105. *V. yersiniana* Guillaumin & Sigaldi in Bull. Mus. Hist. Nat. sér. 2, 36: 162 (1964). Type: VIETNAM (Annam), road from Yersin to Hon ba, Suoi Dao, cult. Suoi Dao, May 1963, *de Sigaldi 362* (syn. P) & 309 (syn. P).

DISTRIBUTION: Thailand, Vietnam.

A common species in Indochina which is readily distinguished by its lanceolate, long-acuminate leaves and whitish flowers with scarcely developed papillae on the lip apex. The narrow, elongate funnel-shaped flowers are different from those of most other Asian species, except its close allies *V. montana*, *V. albida* and *V. andamanica*. Good photographs and illustrations can be found in Seidenfaden and Wood (1992) and Seidenfaden (1978, fig. 87) who considered

it as conspecific with *V. albida*, a different species from Java. *V. albida* has greener tepals and different papillae at the apex of the lip (see pictures in Comber, 1990).

COLLECTIONS: THAILAND: *Larsen & Larsen 33174* (AAU! K!); *Kerr 0805* (K!), *0805A* (K!), *s.n.* (K!); *Hull 671* (K! sterile).

SOURCES: Seidenfaden, G. & T. Smitinand 1959. The Orchids of Thailand: a preliminary list, part 1: 60 (as *V. sp. Kerr 805* and *805A*); Seidenfaden, G., 1978. Orchid Genera in Thailand VI. Dansk Bot. Arkiv. 32(2): 140-141, fig. 87; Averyanov, L.V. 1994. Identification Guide to Vietnamese Orchids: 76 (as *V. albida*); Seidenfaden, G. & J.J. Wood, 1992. Orchids of Peninsular Malaysia and Singapore pages?? Comber, J.B. 1990. Orchids of Java: 76; Averyanov, L.V., N.T. Hiep, P.K. Loc & A.L. Averyanova. Preliminary orchid checklist of Cao Bang Province. Lindleyana 15(3): 163 (as *V. albida*).

106. *V. zanzibarica* Rolfe in Bull. Misc. Inform. Kew 1906: 116 (1906). Type: ZANZIBAR, on the Wanda, near Dunga, *Lyne s.n.* (holo. K!).

DISTRIBUTION: ?Uganda, Kenya, Tanzania, including Zanzibar and Pemba.

Vanilla zanzibarica has been treated as a synonym of *V. ramosa* (e.g. Cribb, 1984; Stewart, 1996). However, the specimens from East Africa usually have much broader leaves, the midlobe of the lip is broader, obtuse, apiculate and conduplicate, and the total length of the lip is longer (up to 25 mm long). The conduplicate lip is more similar to that of *V. crenulata*, although not so high and gibbose, but *V. zanzibarica* lacks the foliaceous bracts of *V. crenulata*. Leaf shape and size approach those of *V. ramosa*, but the flowers are much larger. *Vanilla zanzibarica* seems to be geographically separated from the other members of this complex, being restricted to a small area in the Usambaras, Pemba and Zanzibar in Tanzania and to the Shimba Hills in Kenya.

COLLECTIONS: TANZANIA: *Moreau 408* (K!); *Holtz 159* (K!); *Greenway in Moreau 408A* (K!); *Greenway 4684, 7043* (K!); *Mücke s.n.* (K!); *Zimmermann s.n.* (K!); *Borhidi et al. 86353* (K!).; Zanzibar, *Vaughan 1254* (K!); *Williams 64* (K!); *Fawcraas 3121* (K!); *Greenway 1297, 2606* (K!); *Toms s.n.* (K!). Pemba, *Soaper H45/30* (K!); *Williams 110* (K!). KENYA: *Luke*

3847 (K!); Luke & Robertson 2393 (K!); Magogo & Glover 583 (K!).

SOURCES: Portères, R. 1954. Le Genre *Vanilla* et ses Espèces: 200-201; Cribb, P. 1984. Flora of Tropical East Africa. Orchidaceae 2: 261, 263 (as *V. ramosa*); Stewart, J. 1996. Orchids of Kenya: 89-90 (as *V. ramosa*).

EXCLUDED AND POORLY UNDERSTOOD SPECIES

Vanilla carinata Rolfe in J. Linn. Soc. Bot. 32: 468 (1896). Type: BRAZIL. Organ Mountains, *Miers s.n.* (holo. K!).

The type of this species consists of a single sheet with several poorly-preserved, large flowers (sepals up to 7 cm long) and no leaves or stems. The rachis bears two ovaries with a conspicuous calyculus, and the lip seems to be longer than sepals. It could be *V. chamissonis* or perhaps *V. vellozii*, but the material is insufficient to determine its correct identity. We are inclined to think that the "strongly keeled" lip apex described by Rolfe is an artifact due to the poor preservation of the flowers.

Hoehne (1945) listed it as a synonym of *V. planifolia*.

Vanilla taiwaniana S.S. Ying in Quart. J. Chinese Forest. 20, 2: 55 (1987). Type: Taiwan, Taichuang, July 1984, *F.S. Ho s.n.* (holo. not located).

A poorly known species. The short description suggests that it could be a synonym of *Erythrorchis ochobiensis* (Hayata) Garay, but with its green colour and developed leaves it may belong to a *Pseudovanilla*.

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***COMPARETTIA SOTOANA* (ORCHIDACEAE: ONCIDIINAE), A NEW ECUADORIAN SPECIES**

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ABSTRACT. A new species of *Comparettia*, *C. sotoana*, is described and illustrated from the province of Morona-Santiago, in southeastern Ecuador. *Comparettia sotoana* is compared with *Comparettia langkastii*, from which it mainly differs by the laterally flattened leaves, the subumbellate (vs. distichous), several-flowered (vs. 2-flowered) inflorescence, the short, straight sepaline spur (vs. long, curved), and the ovate-subpandurate lip with a cuspidate midlobe (vs. pandurate with a deeply retuse, apiculate midlobe) provided with digitate-conical basal processes, uncinately at apex and expanded into rounded knobs (vs. straight, acuminate), and lacking apical calli (present in *C. langkastii*).

RESUMEN. Se describe e ilustra una nueva especie de *Comparettia*, *C. sotoana*, de la provincia de Morona-Santiago en la región suroriental de Ecuador. *Comparettia sotoana* se compara con *Comparettia langkastii*, de la cual difiere particularmente por las hojas lateralmente aplanadas, la inflorescencia umbelada (vs. dística) de varias flores (vs. biflora), el espolón sepalino corto y recto (vs. largo e curvo) y el labelo ovado-subpandurado con un lóbulo mediano cuspidado (vs. pandurado con lóbulo mediano profundamente retuso y apiculado), provisto de procesos basales digitado-cónicos, apicalmente en forma de garfio y ensanchados en terminaciones globosas (vs. rectos, agudos) y carente de callos apicales (presentes en *C. langkastii*).

KEY WORDS: Orchidaceae, Oncidiinae, *Comparettia*, *C. sotoana*, new species, Ecuador

Some of the genera of the subtribe Oncidiinae, belonging to the so-called *Rodriguezia* clade, variously treated as the Subtribes Comparettiinae Schltr. (i.e., Szlachetko, 1995) and Ionopsidinae Pfitzer (i.e., Senghas, 1995), had a complex taxonomic history, with many species moving forth and back to alternative genera. This has been particularly true for the genera close to *Scelochilus* Schltr., including *Neokohleria* Schltr., *Scelochiloides* Dodson & M.W. Chase, and *Scelochilopsis* Dodson & M.W. Chase, which have been traditionally difficult to characterize in terms of morphological features. A first attempt to reflect natural relationships through nomenclature was done by Dodson and Chase (*in Brako & Zarucchi*, 1993), who reduced *Neokohleria* under *Scelochilus*. The generic circumscription of *Scelochiloides* has been also subjected to different interpretations, with species of this genus assigned to both *Neokohleria* (Senghas 2001), and *Scelochilus* (Königer 2008).

Vegetative architecture is amply variable among members of the highly derived *Rodriguezia*-clade. Many of the genera as traditionally circumscribed include a vast array of modifications in plant organization, often with retention of pedomorphic traits in the adult psygmoid habit and reduction of pseudobulb size, and leaf shape. Within the clade, the genera *Ionopsis* Kunth, *Neokoehleria*, *Rodriguezia* Ruiz & Pav., and *Scelochilus*, include species with conduplicate, subterete, and/or laterally flattened leaves. On the other side, subtle variations in floral features have been emphasized to circumscribe genera in the group. *Neokoehleria* was basically distinguished from *Scelochilus* by the shape of the sepaline spur (club-shaped vs. conical), and *Scelochiloides* was defined by the presence of a single nectariferous horn at the base of the lip (vs. 2 in *Scelochilus*), while *Scelochilopsis* was characterized by the lack of spur at the base of the lip (Dodson 1998). Eventually, the molecular

studies carried out by Chase, Williams and co-workers (Williams *et al.* 2001a, 2001b, Sosa *et al.* 2001, Chase 2009), aimed to reconstruct a phylogenetic scheme of relationships within the Oncidiinae, revealed that the genera centered around *Comporettia* are all embedded within *Scelochilus*. Morphologically, taxa in this group only differ in subtle details of their nectar horns and the relative length of the spur that embrace them. In order to accord nomenclature with the molecular findings, Chase *et al.* (2008) combined all the species of this group provided with short spur, previously treated as the genera *Chaenanthus* Lindl., *Diadenium* Poepp. & Endl., *Neokoehleria*, *Pfizeria* Senghas, *Scelochilopsis*, *Scelochilus*, and *Stigmatorthos* Dodson & M. W. Chase, into the single genus *Comporettia*.

During the ongoing work aimed to the documentation of orchid species in the collection of Ecuagenera, to be accessed to the living collection and ancillary collections of the Andean Orchid Research Center (CIOA by its acronym in Spanish), University Alfredo Pérez Guerrero, we discovered a new species of *Comporettia* that we describe here as new to science:

Comporettia sotoana Pupulin & G. Merino, *sp. nov.*

TYPE: ECUADOR. Morona Santiago: Tumbes, 1200 m, collected by G. Merino, 15 February 1993, cultivated by Ecuagenera at Gualaceo, accession No. CIOA-00527, flowered 19 March 2008, *F. Pupulin 7063* (holotype, QCA-Spirit). Fig. 1.

Species *Comporettiae langkastii* (Senghas) M.W. Chase & N.H. Williams similis, inflorescentiae multiflorae subumbellata, calcar sepalino brevis recto, labello ovato-subpandurato lobo medio cuspidato, processibus basalibus digitato-conicis apicaliter uncinatis globosis instructo, callibus apicalibus destituto recedit.

Epiphytic, erect, caespitose *herb.* *Roots* slender, flexuous, *ca.* 1 mm in diameter, produced from the rhizome under the pseudobulb. *Pseudobulbs* small, 4 mm in diameter 5 mm long elliptic, complanate, monophyllous at apex (or with a second, apical, small, lanceolate leaflet), partially concealed at the base by the bases of 2–3 foliaceous sheaths, the sheaths 6–10 mm long, articulated with the leaf. *Leaves* laterally flattened (equitant), lanceolate, slightly asymmetrical,

acute, minutely mucronate, thick-coriaceous, green suffused with purple, 3.5–7.0 x 0.4–0.8 cm, the larger ones provided with a subcylindric petiole to 5 mm long. *Inflorescence* lateral, arising from the axil of a sheath, a few-flowered (to 5), congested, subumbellate raceme to 3 cm long; peduncle erect, terete, to 2 cm long, with 1–2 strongly conduplicate, laterally flattened, lanceolate bracts, 6 x 3 mm; floral bracts lanceolate, glumaceous, 4.0–6.0 x 1.5 mm. *Ovary* terete, to 8 mm long including the pedicel. *Flowers* not completely spreading, campanulate, the sepals pale yellow, the petals greenish white suffused with orange, the lip white spotted orange, the column pale yellow, the anther white. *Dorsal sepal* elliptic-oblongate, obtuse, concave, reclined over the column, 4.6 x 2.5 mm. *Lateral sepals* connate for about 3 mm into an elliptic, concave synsepal, 5.8 x 3.0 mm, the free apices obtuse to subacute, extending at the base into a sepaline, saccate spur *ca.* 2 mm long. *Petals* elliptic, asymmetrical, rounded, apiculate, slightly concave, 5 x 3 mm. *Lip* 3-lobed, ovate-subpandurate, canalculated, the lateral lobes elliptic, rounded, suberect; the midlobe cuspidate, slightly conduplicate; the base of the lip protruding toward the rear into two digitate-conical processes, uncinata at apex and expanded into rounded knobs, 2 mm long; disc with 2 low, subquadrate, diverging calli. Column straight, ascending, subterete, thicker toward the apex, 3.7 mm long, provided with broad elliptical wings; stigma rounded. *Anther cap* cucullate, subquadrate, 2-celled. *Pollinia* 2, elliptic-obovate, complanate, on a spatulate-subflabellate, hyaline stipe, viscidium and an ovate viscidium. *Fruit* not seen.

EPONYMY: dedicated to Miguel Angel Soto Arenas, for his outstanding contributions to Neotropical orchidology.

DISTRIBUTION AND ECOLOGY: Known exclusively from Ecuador. Populations of *C. sotoana* grow epiphytically in open shade in wet forests in the province of Morona Santiago at approximately 1200 meters of elevation, where they are apparently restricted to the terminal branchlets of secondary vegetation. Plants have been found in flower from February to March.

Dodson (2004) first published a photograph of *C. sotoana*, as an unnamed species of *Scelochilus*,

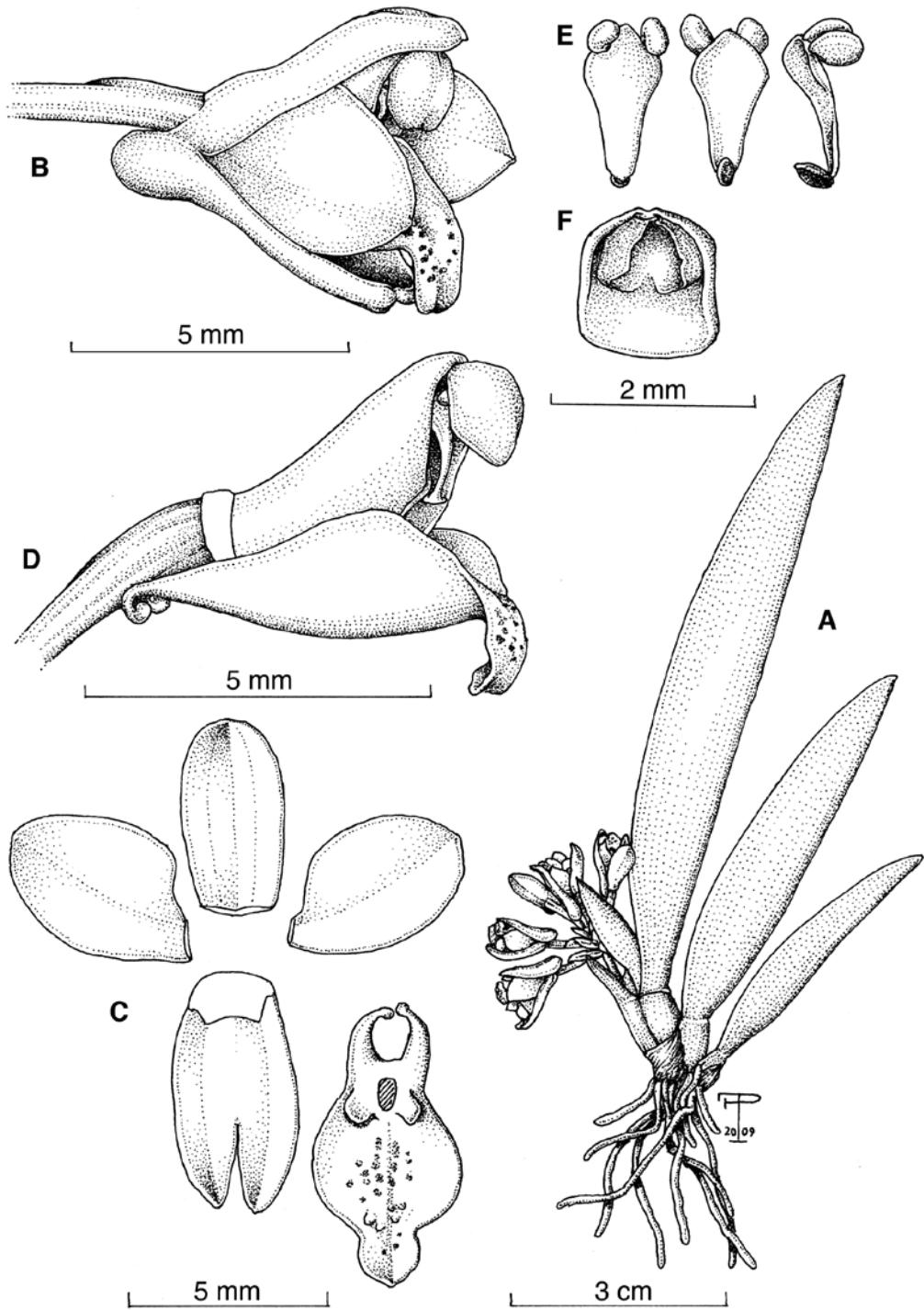


FIGURE 1. *Comparettia sotoana* Pupulin & G.Merino. A — Habit. B — Flower. C — Dissected perianth. D — Ovary, column and lip, lateral view. E — Pollinarium, three views. F — Anther cap, ventral view. Drawn by F. Pupulin from the holotype.

on the basis of an Ecuadorian collection by A. Hirtz (8134, probably at RPSC, now at MO). *Comparettia sotoana* belongs to a small group of species, mostly previously included in *Neokoehleria*, known from the Amazonian basin and the eastern slopes of the Andes from Colombia to Peru and Bolivia. Among them, *C. sotoana* is most similar to *C. langkastii* (Senghas) M.W. Chase & N. H. Williams, also endemic to Ecuador. It differs from *C. langkastii* in several characters, including the shape of pseudobulb (elliptical-subcylindrical vs. rounded-complanate) and the leaves (laterally flattened vs. strongly conduplicate-triquetrous), the subumbellate (vs. distichous), several-flowered (vs. 2-flowered) inflorescence, the short (<3 mm vs. >5 mm long), straight (vs. curved) sepaline spur, and the ovate-subpandurate lip with a cuspidate midlobe (vs. pandurate with a deeply retuse, apiculate midlobe) lacking apical calli (present in *C. langkastii*). Furthermore, the nectariferous horns at the base of the lip of *C. sotoana* are digitate-conical, uncinata at apex and expanded into rounded knobs, while in *C. langkastii* they are straight and apically acuminate.

ACKNOWLEDGEMENTS. We are grateful to José “Pepe” Portilla and his family for allowing us free use of the plants in the collection of Ecuagenera and for giving us any kind of facilities at Gualaceo. To the Ministry of Environment of Ecuador for extending the management permits of the living collections where the species treated here have been documented. To the Foundation for Orchid Research and Conservation, Vancouver Orchid Society, Canada, for its kind sponsoring of the AORC. The present paper is part of the Project 814-A7-015, “Inventario y taxonomía de la flora epífita de la región Neotropical — Orchidaceae”, sponsored by the Vice-Presidency of Research, University of Costa Rica.

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CONFUSION IN *EPIDENDRUM BRENESII* SCHLTR., AND A NEW COSTA RICAN SPECIES: *EPIDENDRUM SOTOANUM* (ORCHIDACEAE)

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ABSTRACT. Two species have been confused under the name *Epidendrum brenesii* Schltr., both were used in the original description and drawing of the type. The purple-flowered species, has been commonly known as *E. brenesii*, a specimen collected by Brenes close to the original *locus typicus* is therefore used to neotypify the species. The yellow-flowered species is described as *Epidendrum sotoanum* Karremans & Hágsater, in honor of the late Mexican botanist Miguel Ángel Soto Arenas.

KEY WORDS: *Epidendrum brenesii*, *Epidendrum sotoanum*, Costa Rica, Miguel Ángel Soto Arenas

A couple of years ago, while collecting above Muñeco, Cartago, Costa Rica, Diego Bogarín and his companions of the Lankester Botanical Gardens, collected a plant which resembled *Epidendrum brenesii* Schltr., because of its characteristic vertical growth habit, with successive lateral growths produced from the middle of the previous growth, and roots produced usually only from the base of the primary stem. After flowering, Karremans noted that it did not have the expected deep purple, velvety lip, but rather a larger, greenish yellow, glabrous lip, deeply cleft at the apex (Fig. 1).

Hágsater, upon seeing the images, immediately remembered a manuscript sent to him in 1983 by Kerry Barringer and Eric Christenson, proposing a yellow-flowered *Epidendrum* as new, but which he considered at the time to corresponded to *E. brenesii*. The matter slept for 16 years in a drawer.

Investigating the case further, all the material under *E. brenesii* was reevaluated to determine the presence of possible confused specimens. We have searched the AMO files, and found not only that Luis Sánchez, of AMO had also collected a specimen which later flowered in cultivation, but images of the original material pressed by Barringer and Christenson, and several Skutch and Standley specimens, corresponding to the eastern part of the range of what went for *E. brenesii*, were all marked as having yellow-brown flowers, and came from the

upper basin of the Río Reventazón. More studied specimens collected further west all showed yellow-flowers as well.

It was obvious that a detailed re-evaluation of the original description and tracings of the type of *Epidendrum brenesii*, lodged at AMES, was necessary (The original type material was destroyed in Berlin during the war). It immediately became evident that both the illustration and the description are a composite of two different flowers. The illustration of the flower shows an entire flower with a relatively narrow, reniform, short-emarginate lip that corresponds to the purple-colored species. On the other hand, the floral segments present a very wide lip with a very wide sinus; the lines in the middle of

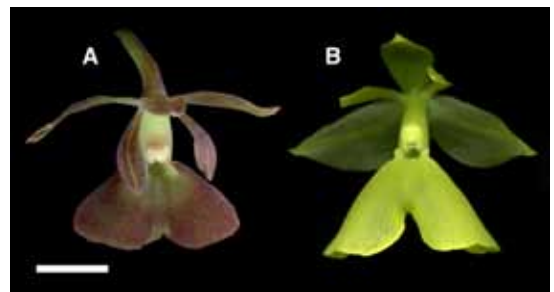


FIGURE 1. Comparison of the living flowers of, A – *Epidendrum brenesii* Schltr. (Bogarín 1513) and B – *Epidendrum sotoanum* Karremans & Hágsater (Bogarín 3920). Scale bar = 1 cm. Photo by F. Pupulin (A) and D. Bogarín (B).

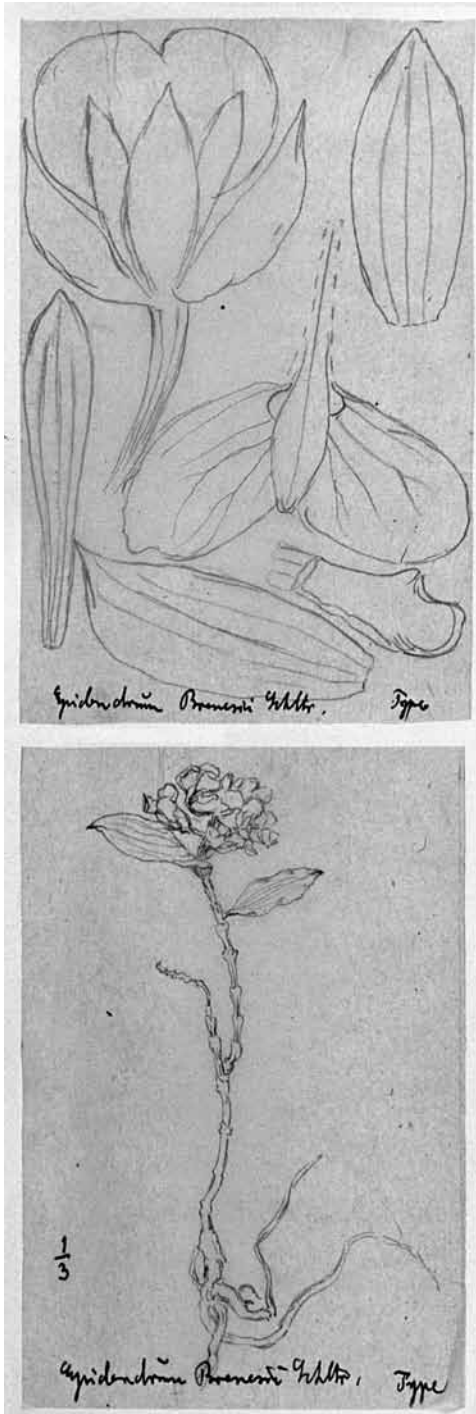


FIGURE 2. Drawing of the holotype of *Epidendrum brenesii* (AMES), from *Brenes 118*. Courtesy of the Orchid Herbarium of Oakes Ames, Harvard University Herbaria.

the lip suggest a pair of keels running down the disc to the apex; features which correspond to the yellow-colored species. The drawing of the plant habit clearly illustrates the typical architecture of this group within *Epidendrum*, but is not useful to distinguish between the two entities (Fig. 2).

The original description indicates that the flowers are light green, tinged with violet, which is what has traditionally been called *E. brenesii*. However, the text indicates that the lip is widely reniform, nearly twice as wide as it is long (15 x 8 mm), that it is widely emarginate, and that the flowers are glabrous (Schltr. 1923). Those features correspond to the yellow-flowered species.

It is thus evident to us that Schlechter made a composite description and the unpublished illustration of the floral parts is also a composite. It could have happened when the floral parts were put together for the purpose of publishing the floral analysis; the view of one flower got mounted with the floral segments of another. Later, when Santiago & Hågsater (2006) published their revision of *E. brenesii* in *Icones Orchidacearum*, though the illustration was prepared from one single specimen of purple-colored flowers, they also prepared a composite description covering all the material then thought to belong to a single species, with either yellow or purple flowers.

Another distinguishing feature is the surface of the lip in the purple-colored species, which is clearly velutinous in fresh flowers, and can be seen under the microscope to be short-setose, densely covered by short, pointed trichomes. The yellow-flowered species has a glabrous appearance, the surface covered with low, rounded papillae.

Upon mapping all the collection localities, the purple-colored species appears to be endemic to the Cordillera Central, from the upper ridge south, while the yellow-colored species ranges along the Atlantic slope east as far as the upper basin of the Río Reventazón. Both species are present in the region of Varablanca.

After viewing all available evidence, we hereby propose to fix the type of the purple-flowered species with a neotype, using another specimen collected by Brenes near the type locality and located in the National Herbarium in San José, Costa Rica:

Epidendrum brenesii Schltr., Repert. Spec. Nov.

Regni Veg. Beih. 19: 209. 1923.

TYPE: COSTA RICA. Alajuela: San Pedro de San Ramón, 1050 m, November 1921, *A. M. Brenes 118*. Holotype: B (destroyed). Lectotype (designated by E. Santiago & E. Hágsater, in E. Hágsater & L. Sánchez S., Icon. Orch. (Mexico City) 8: pl. 814. 2006.): tracing of the type with floral details, mounted on *Standley 36573*, AMES 29339! (Cited by Barringer, 1986.), here rejected. Neotype (here designated): COSTA RICA: Alajuela: La Palma de San Ramón, 1250 m, 14 November 1922, *Brenes 449(154)*, CR!

Epiphytic, monopodial, erect herb, 30-70 cm tall. Roots basal from the initial stem and sometimes from an upper stem, 1.5-3 mm thick. Stems simple, cane-like, terete, straight, the new stem originating from a middle internode of the previous stem, gradually becoming thinner and shorter, 5-30 x 0.2-0.5 cm. Leaves 3-5, aggregate along the apical half of the stem, alternate, articulate, erect-spreading, unequal in size, the basal one generally smaller, sub-coriaceous; sheaths tubular, minutely striated, becoming fibrous with time, light green tinged with purple, 11-17 mm long; blade oblong, acute, margin entire, 2-8 x 1.3-2.5 cm. Inflorescence apical, flowering only once, racemose to rarely paniculate, arching, 2-4 cm long; peduncle thin, laterally compressed, straight, light green tinged purple, 1.0-1.5 cm long. Floral bracts about half as long as the ovary, triangular, acuminate, tinged purple, 4-5 mm long. Flowers 8-12[40], successive, though several may be open at one time, resupinate, light green with purple tinge to deep purple with the column green; slight “banana-peel” fragrance at sundown. Ovary terete, thin, not inflated, smooth, tinged purple, 8-13 mm long. Sepals partly spreading, free, obovate-elliptic, acute, slightly concave, glabrous, 3-veined, margin entire, spreading, dorsal sepal 12-13 x 6.0-6.5 mm, laterals oblique, 14.5-15.0 x 7.5 mm. Petals partly spreading, free, linear-oblong, acute, 3-veined, margin entire, spreading, 12 x 2.5-3 mm. Lip united to the column, entire, reniform, slightly convex, velutinous, short setose, densely covered by short, pointed trichomes, emarginate, the apex sometimes slightly 4-lobed, margin entire, 8-12 x 15-19 mm; bicallose, the calli formed by a pair of short, laterally compressed thickenings; disc with a low, wide keel

that reaches the apical sinus. Column thin at the base, gradually widened towards the apex, straight, 6.5 mm long; clinandrium-hood reduced, the margin erect, entire; rostellum apical, slit. Anther subreniforme, 4-celled. Pollinia 4, obovoid, laterally compressed, caudicles soft and granulose, as long as the pollinia. Nectary penetrating somewhat the ovary, smooth.

MATERIAL STUDIED: COSTA RICA. Alajuela: La Palma de San Ramón, 1250 m, 8 III 1930, *Brenes 11909a*, NY! Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, 1500-2000 m, cult. XII 2007, *Karremans 2188*, JBL-Spirit! Digital image, AMO! JBL! Sarapiquí, 8 II 1966, *Lankester s.n. sub Rodriguez 366*, USJ! (Illustration voucher). Heredia: Montaña Azul, entre Vara Blanca y Cariblanco, col. 19 III 1982, pressed cult. 23 I 1983, *Hágsater 6822*, AMO! Varablanca-Cariblanco, Montaña Azul, col. 19 III 1982, pressed cult. 22 II 1983, *Hágsater 6824*, AMO! (Illustration voucher, Fig. 3). Vara Blanca, 2 km noreste de Alto del Roble, faldas al norte del Cerro Chompipe, Refugio de Vida Silvestre Cerro Dantas, márgenes de la Quebrada Grande, 10°5'30.5"N 84°03'51.4"W, 1981 m, 14 IV 2005, *Bogarin 1513*, JBL-Spirit! Digital image, AMO! JBL! Vara blanca, cerca del cruce a San Miguel, 1000 m, 28 X 1995, *Morales 4966*, INB!

OTHER RECORDS: COSTA RICA. Alajuela: Valverde Vega, Bajos del Toro, *Karremans s.n.*, digital photo AMO! JBL! Sarapiquí, 11 II 1966, *Lankester s.n. sub Rodriguez 366*, xerox of illustration, AMO!

DISTRIBUTION AND ECOLOGY: Endemic to central Costa Rica, known only from the upper ridge of the Cordillera Central and south towards San Ramón, in humid premontane forest at 1000-2000 m altitude. Flowering from October to April.

We further propose the yellow-flowered species as new:

Epidendrum sotoanum Karremans & Hágsater, sp. nov.

TYPE: COSTA RICA: Cartago; Finca Kiri, camino a la Reserva Natural de Tapantí, 1300-1400 m, col. 25 IX 1996, pressed 12 VI 1998, *L. Sánchez 401*, *J. García Cruz, D.E. Mora & O. Rodríguez*. Holotype: USJ! Clonotype: Ibid. pressed 19 V 1997, AMO!

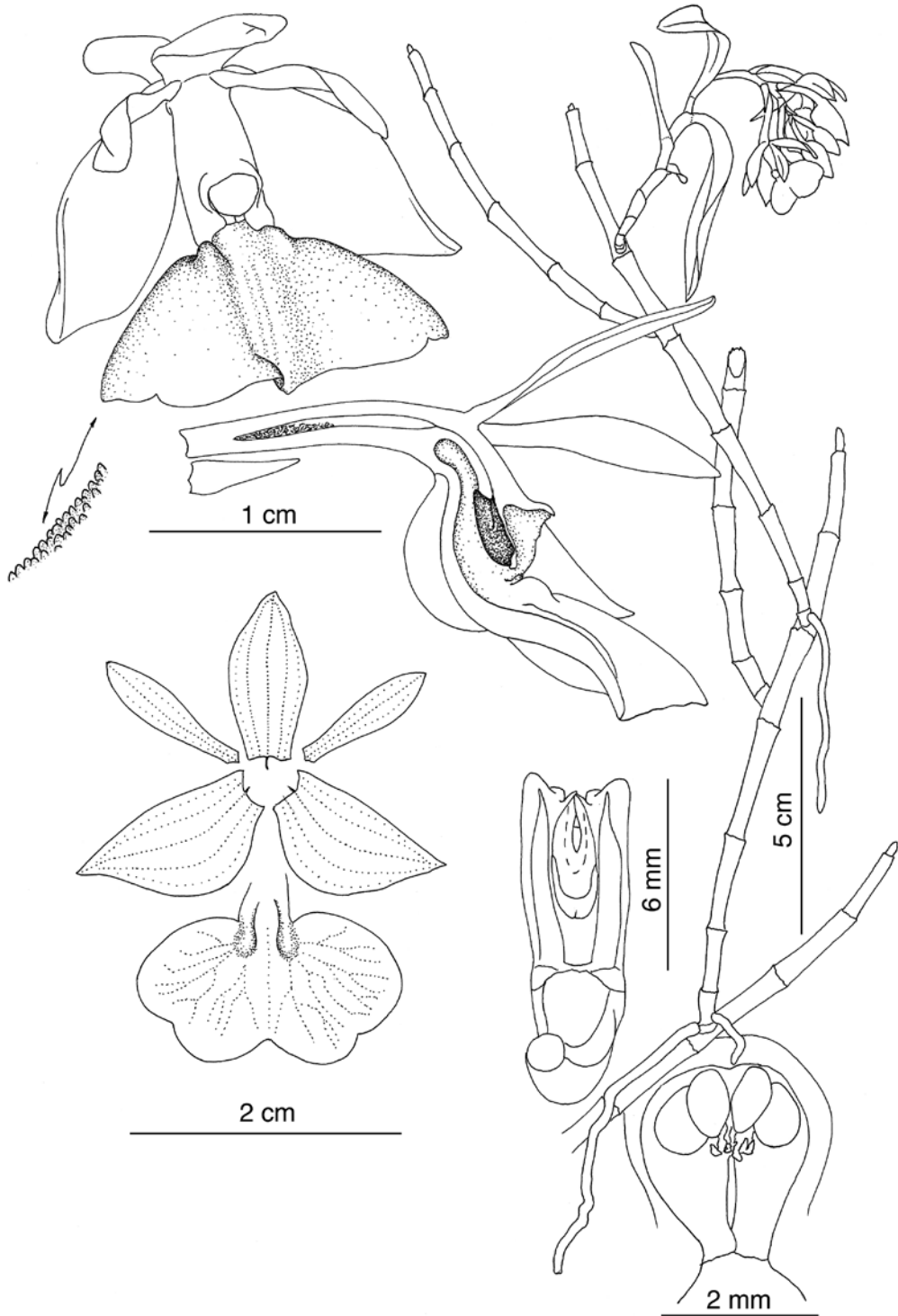


FIGURE 3. *Epidendrum brenesii* Schltr. A – Flower. B – Habit. C – Column and lip, lateral view. D – Dissected perianth. E – Column, ventral view. F – Pollinarium. Drawn by E. Hågsäter from *Hågsäter 6824* (AMO).

Species *Epidendro brenesii* Schltr. similis, floribus glabris flavis vel viridis plus minusve brunneo maculatis, labello latiore profunde et late emarginato recedit.

Plant epiphytic, monopodial, erect, branching, up to 50 cm tall. *Roots* basal, from the basal stem only, fleshy, filiform, thick. *Stems* terete, somewhat flexuous, each new stem produced from a subapical internode of the previous stem, below the leaves. *Leaves* few (3 in the holotype), aggregate towards the apex of the stem; sheath tubular, rugose; blades obovate-elliptic, obtuse, variable in size, the largest up to 5-10 x 1.3-2.5 cm. *Inflorescence* apical, flowering only once from each stem; peduncle laterally compressed and somewhat ancipitose, 2 cm long. *Floral bracts* half as long as the ovary, acute, 0.6-1 cm long. *Flowers* 4-15, greenish brown or yellow, column green, darker at the base. *Ovary* terete, smooth. *Sepals* partly spreading, obovate-elliptic, obtuse, 3-4-veined, margin entire, spreading; dorsal sepal 12-16 x 4.0-7.5 mm, lateral sepals oblique, 13-18 x 7-9 mm. *Petals* partly spreading, narrowly-obovate, obtuse, 3-veined, margin entire, spreading, 11-15 x 2-4 mm. *Lip* strongly bilobed, widely reniform, deeply emarginate, slightly convex in natural position, superficially glabrous in appearance but with low rounded papilla when observed under a microscope, 10-17 x 20-30 mm; lateral lobes obscurely bilobed, sub-orbicular, sometimes emarginate; margin entire; bicallose, the calli thickened at the base and ending in a pair of low keels. *Column* somewhat arching downwards, short, thickened towards the apex, sub-terete, 7-8 x 5 mm above the middle, with apical rounded wings; clinandrium-hood erect, very short, margin entire; rostellum near the apex of the column, slit. *Anther* obovate, 4-celled, 2.5 mm wide. *Pollinia* 4, obovoid, laterally compressed. *Nectary* short, without penetrating the ovary, smooth.

MATERIAL STUDIED: COSTA RICA. Cartago: Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1430-1620 m, bosque pluvial premontano, epífitas bosque secundario y árboles en zonas abiertas, 23 V 2007, *Bogarín 3919*, M. Bonilla, R. Gómez, R. Trejos & J.D. Zúñiga; JBL-Spirit! Digital image, AMO! JBL! (Illustration voucher, Fig. 4). Ibid. *Bogarín et al. 3920*, JBL-

Spirit! Digital image, AMO! JBL! Orosi valley, in orchard along timber road above El Muñeco, along Rio Sombrero, 1500 m, 9°47'N, 83°11'W, 6 VI 1983, *Barringer & Christensen 4167*, F! Digital image and illustration, AMO! Heredia: San Rafael, Rio Tibas, toma de agua de Concepción de San Rafael, 1700 m, 2 XII 1995, *Lépiz 160*, INB! Vara Blanca de Sarapiquí, between Poás and Barva volcanoes, 1770 m, II 1938, *Skutch 3510*, AMES! Ibid. 1950 m, II 1938, *Skutch 3526*, AMES! K! MO! Yerba Buena, NE of San Isidro, 2000 m, 22 II 1926, *Standley 49987*, AMES! US! Vara Blanca, 1400-1700 m, 27 VI 1978, *Todzia 332*, CR! **San José:** La Hondura, 1300-1700 m, 2 III 1924, *Standley 36573*, AMES! US!

OTHER RECORDS: COSTA RICA. Alajuela: San Pedro de San Ramón, 1050 m, XI 1921, *Brenes 118**, B (destroyed), tracing of the floral details excluding the view of the whole flower; mounted on *Standley 36573*, AMES 29339! (Cited as type of *E. brenesii* by Barringer, 1986 and designated as lectotype of by Santiago & Hágsater, 2006). Cartago: Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1430-1620 m, bosque pluvial premontano, epífitas bosque secundario y árboles en zonas abiertas, 23 V 2007, *D. Bogarín 3819*, M. Bonilla, R. Gómez, R. Trejos & J.D. Zúñiga, Digital image, AMO! JBL!

DISTRIBUTION AND ECOLOGY: Endemic to Costa Rica, on the Cordillera Central, along the Atlantic slope, and east to the upper basin of the Río Reventazón. Epiphytic in secondary humid premontane forest, at 1500-2000 m elevation. Flowering in December-June.

Epidendrum sotoanum belongs to the Arbuscula Group, Incomptum Subgroup, which is characterized by the successive lateral growths produced from the middle of the previous growth, few leaves which aggregate towards the apex of the stems, a short apical inflorescence with fleshy greenish to violet-green flowers with short ovaries, the lip entire to 3-lobed. The

* The illustration and original description of *E. brenesii* represent a mixed collection, the floral segments belong to this entity, but the image of the entire flower to *E. brenesii*; the illustration of the plant habit is indistinguishable.

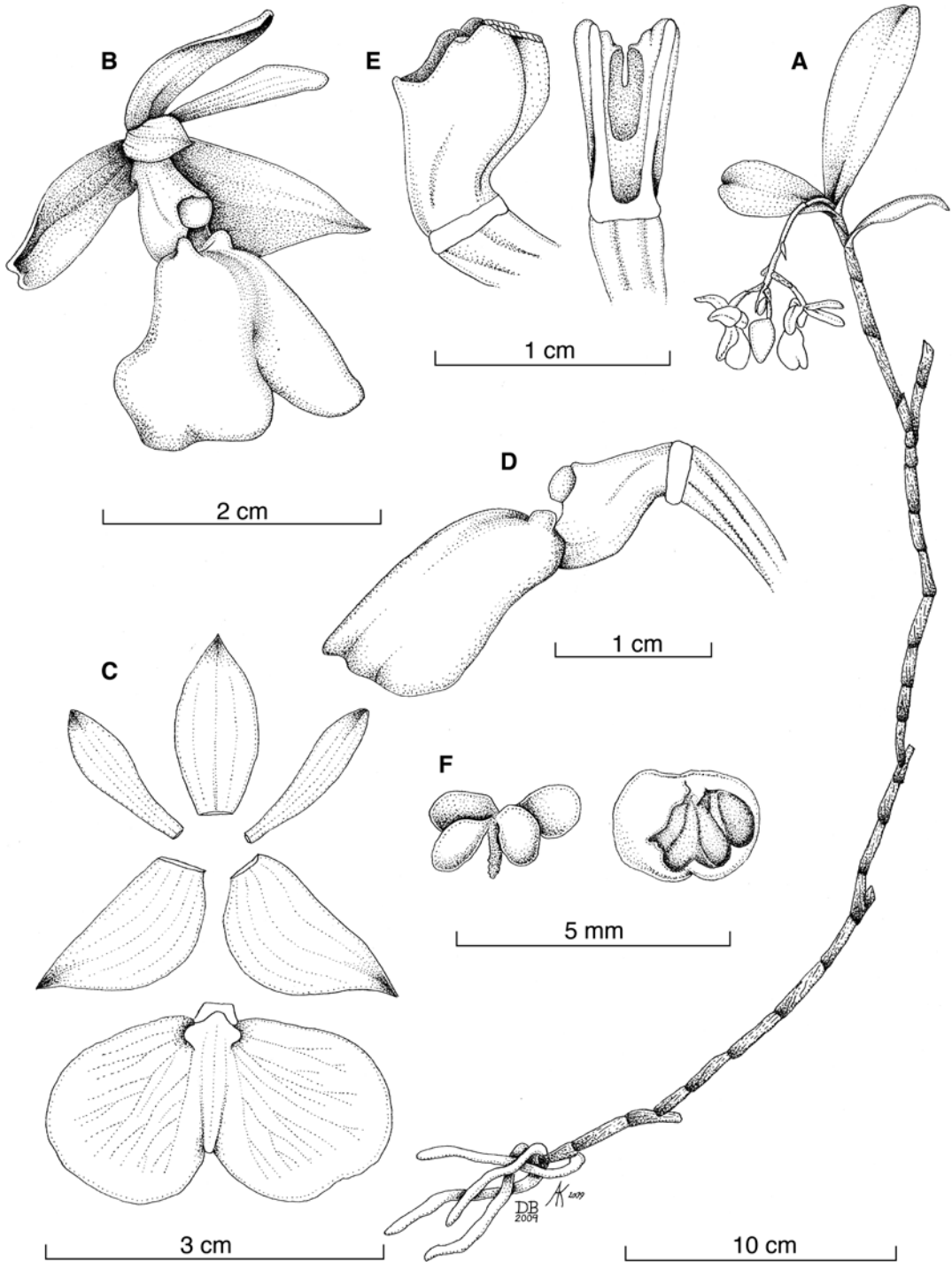


FIGURE 4. *Epidendrum sotoanum* Karremans & Hągsater. A – Habit. B – Flower. C – Dissected perianth. D – Column and lip, lateral view. E – Column, side and frontal views. F – Pollinarium and anther cap. Drawn by A. Karremans & D. Bogarín from Bogarín 3919 (JBL-Spirit).

species is recognized by the large greenish yellow or greenish brown flowers, the glabrous (microscopically papillose), very large, deeply emarginate lip, and the apical rounded wings of the column. It is similar and has been confused with *Epidendrum brenesii* Schltr. which is known from upper ridge of the Cordillera Central and south towards San Ramón, its inflorescence has 8-12[40] violet-green flowers, a reniform, velutinous, short-emarginate lip, 15-19 mm wide. *Epidendrum bisulcatum* Ames, has shorter and narrower leaves, a smaller, sub-orbicular lip and linear petals. *Epidendrum incomptum* Rchh.f. which also occurs in Costa Rica can be distinguished by its 3-lobed, ecallose lip, the 3 lobes more or less triangular. Outside Costa Rica, only *Epidendrum foldatsii* Hágsater & Carnevali from Venezuela has the same architecture, and a bilobed lip, but the flowers are small, the lip being 4 x 7.5 mm.

We take pleasure in dedicating this species to our late fellow orchid researcher from Mexico, Miguel Ángel Soto Arenas, (1963-2009) who shared his knowledge and experience with us. Apart from his many contributions to science, reading through the narrative of the different ecosystems in *The Orchids*

of Mexico, gives us a glimpse of how well he came to understand the relationship between orchids and their various habitats, as well as the threats to biodiversity.

ACKNOWLEDGEMENTS: We wish to thank Diego Bogarín (JBL) for sharing his material and knowledge of the species and preparing sketches of the new species, and Elizabeth Santiago (AMO) for once more going through all records, and ample discussion of the manuscript, and revision of the descriptions. We are also thankful to G. Wece (WUR) for the tactical support.

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***ONCIDIUM ORNITHORHYNCHUM*, UNA ESPECIE MAL INTERPRETADA Y UN NOMBRE PARA UNA VIEJA ESPECIE: *ONCIDIUM SOTOANUM* (ORCHIDACEAE)**

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RESUMEN. Se aclara la identidad de *Oncidium ornithorhynchum* Kunth, una especie mal interpretada, debido a que el tipo depositado en el herbario de París (P) no corresponde con la especie que ha recibido ese nombre en México y Centroamérica, sino con un taxón de Ecuador, Colombia y Perú conocido como *O. pyramidale* Lindl. Se propone como nueva a la especie de México y Centroamérica: *O. sotoanum* R.Jiménez & Hágsater y se describe una nueva subespecie: *O. sotoanum* ssp. *papalosmum* R.Jiménez, conocida únicamente de los estados de Oaxaca y Chiapas, México.

ABSTRACT. The true identity of *Oncidium ornithorhynchum* Kunth is identified based on the type found at the Paris herbarium (P). It does not correspond to the well known Mexican and Central American species, but to *O. pyramidale* Lindl. from Ecuador, Colombia and Peru. The Mexican and Central American species is proposed as new: *O. sotoanum* R.Jiménez & Hágsater, and a new sub-species is also proposed, *O. sotoanum* ssp. *papalosmum* R.Jiménez, known only from the states of Oaxaca and Chiapas, Mexico.

PALABRAS CLAVE / KEY WORDS: *Oncidium*, *ornithorhynchum*, *sotoanum*, *papalosmum*, *pyramidale*

Una de las especies más populares de *Oncidium* en México, por sus flores rosadas, fragantes, de fácil cultivo, y abundante floración es la que universalmente se conoce como “*Oncidium ornithorhynchum*”. Su cultivo es sencillo y en unos cuantos años llena su recipiente y presenta numerosas inflorescencias arqueadas en todas direcciones, lo que forma un bouquet perfecto como centro de mesa. Ha sido utilizada también en la creación de numerosos híbridos y clones seleccionados que han recibido reconocimientos en todo el mundo.

Theodor Hartweg envió plantas colectadas en Oaxaca, México, a Loddiges quien la introdujo al cultivo por primera vez en Europa en 1836. Ese año Ure Skinner envió a James Bateman una planta de Guatemala, misma que ilustró en su famosa obra *The Orchidaceae of Mexico and Guatemala* con el nombre de *Oncidium ornithorhynchum* e incluyendo un comentario que posteriormente repitió Lindley (1840), haciendo referencia a la obra de Kunth, el cual menciona que hay copias coloreadas a mano donde las flores de esta especie se representaban de color amarillo; afirmando que seguramente se debía a que el dibujo se hizo a partir de un espécimen seco. Según

Staffeu & Cowan (1979), dichas copias se encuentran en U, BM-Bloomsbury y la Biblioteca Nacional de París.

En la primera entrega de *The Orchidaceae of Mexico and Guatemala* (1837) apareció la especie de México y Centroamérica ilustrada por primera vez como “*O. ornithorhynchum*”. Es probable que la planta dibujada por Bateman haya sido determinada por Lindley, quien la publicó por segunda vez con una nueva ilustración (Lindley, 1840). Es probable que el autor se haya dejado llevar por la ilustración y la localidad de origen mencionada en la obra de Kunth. Además en aquél tiempo la identificación se centraba en la flor, sin mucha atención a la arquitectura de la inflorescencia y el número de estas por pseudobulbo. Todos los autores posteriores a Bateman aceptaron su ilustración como la representación de *O. ornithorhynchum*.

En 1990 Miguel Ángel Soto, tuvo la oportunidad de ver en el herbario de París el ejemplar tipo de *Oncidium ornithorhynchum* y se dio cuenta que la especie que tenemos en México sorprendentemente no correspondía con dicho ejemplar. Lamentablemente no le fue posible fotografiarlo para tener un registro del material. Sin embargo, el hecho quedó grabado en

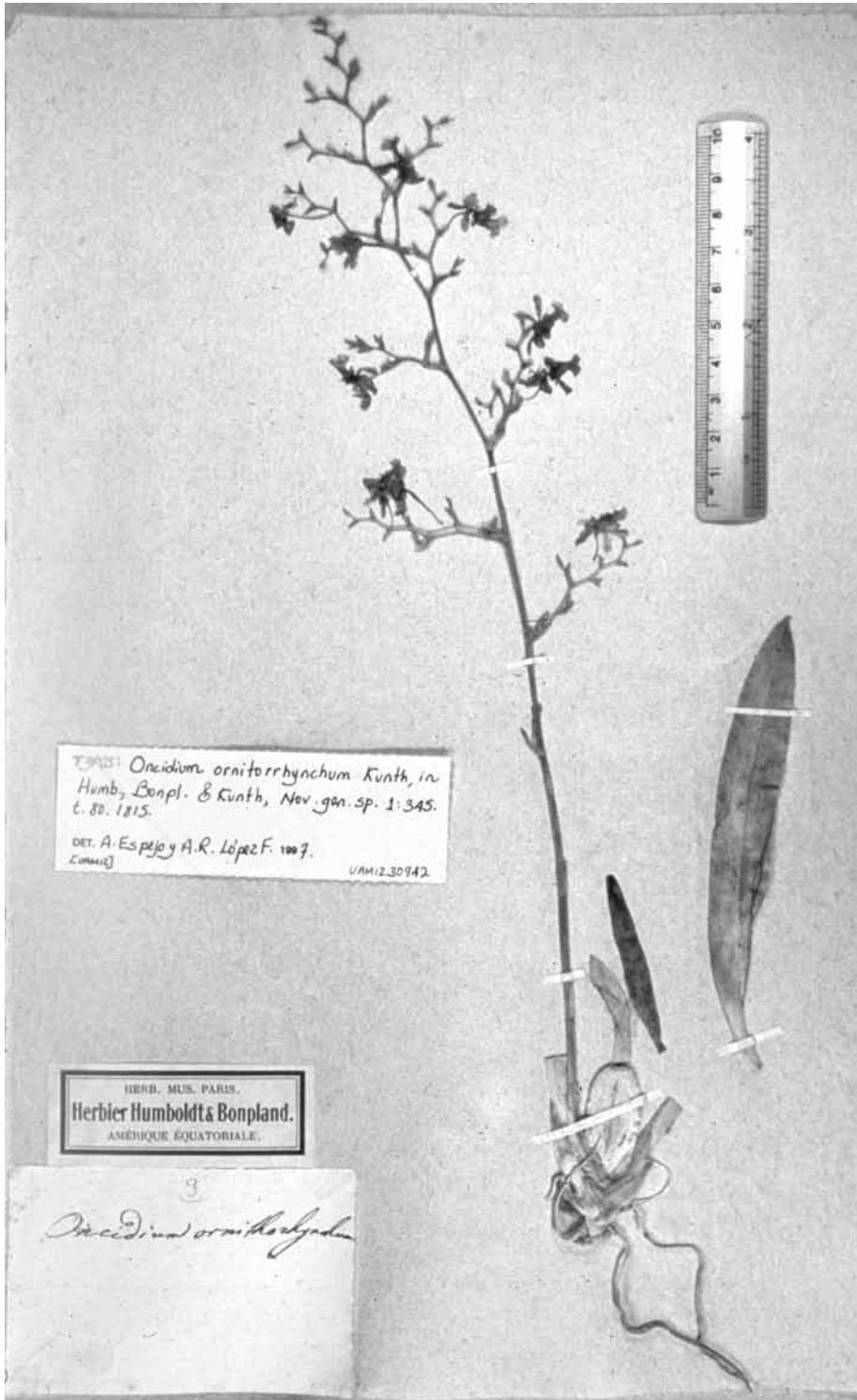


FIGURA 1. Foto del Tipo de *Oncidium ornithorhynchum* Kunth en el Herbario de París. Foto cortesía de A. Espejo Serna.

su memoria y lo comentamos en varias ocasiones. Fue hasta 1997 que Adolfo Espejo, botánico mexicano, viajó a París y obtuvo una fotografía del ejemplar tipo de *O. ornithorhynchum* como parte de su investigación de los tipos de las monocotiledóneas mexicanas (Espejo *et al.* 1998), del cual amablemente nos proporcionó una copia (Fig. 1).

Al examinar los ejemplares tipo de los “oncidiums” mexicanos, Jiménez (2008) confirmó que la especie respaldada por el tipo de *Oncidium ornithorhynchum* Kunth en el herbario de Paris (P), no concordaba con la especie que se distribuye en México y Centroamérica y que se conoce universalmente con este nombre.

Ya con la imagen del tipo en nuestras manos, se procedió a hacer un análisis del ejemplar, así como del protólogo y la lámina que lo acompaña (Fig. 2) para comparar este material con la planta mexicana que se conoce como *O. ornithorhynchum*. El material original muestra que las vainas foliosas de la base del pseudobulbo tienen el margen membranáceo muy evidente; hay una sola inflorescencia por pseudobulbo, erecta, con las ramas de la base alargadas, acortándose gradualmente hacia el ápice (arquitectura piramidal), el pedúnculo y raquis son casi rectos, ligeramente sinuosos; el callo del labelo se compone de dos quillas cortas hacia los lados y otras tres hacia el ápice; las alas de la columna son erectas y cuneadas.

En la especie mexicana las flores son rosadas con el callo amarillo; el margen de las vainas foliosas es membranáceo pero este es inconspicuo, midiendo tan solo 1 mm de ancho. Cada pseudobulbo produce simultáneamente 2-4 inflorescencias arqueado-colgantes. La arquitectura de la inflorescencia presenta las ramas de la base del raquis cortas, las de la mitad largas y las del ápice cortas. El raquis es en zigzag. El callo es distinto y las alas son oblicuamente dolabriformes y paralelas al cuerpo de la columna.

Llama la atención que la localidad tipo de *O. ornithorhynchum* dada por Kunth, “El Puerto Andaracuas, entre Guanajuato y Valladolid, Michoacán”, es evidentemente errónea (Jiménez, 1990). Esa localidad corresponde a la provincia fisiográfica conocida como la Altiplanicie mexicana meridional y El Bajío, una zona muy seca, donde abundan los encinares secos, muy pobres en orquídeas epífitas, siendo la más frecuente *Laelia speciosa* (Hágsater *et al.* 2005).



FIGURA 2. Lámina no. 80 que acompaña la publicación original de *Oncidium ornithorhynchum* en la obra *Nova Genera et Species Plantarum*, la cual se basó en el ejemplar colectado por Humboldt y Bonpland depositado en el herbario de París.

El ejemplar tipo (Fig. 1), tiene una etiqueta con la leyenda “America Ecuatorialis” por lo que no es difícil deducir que el ejemplar probablemente fue colectado en Sudamérica. De acuerdo con las características de la arquitectura “piramidal” de la inflorescencia, las alas de la columna erectas y la estructura del callo, las únicas especies que presentan éstas son *Oncidium pyramidale* Lindl. que se distribuye en Perú, Ecuador y Colombia, y *Oncidium elephantotis* Rchb.f. de Ecuador. *Oncidium elephantotis* tiene una inflorescencia pequeña, con alas de la columna muy amplias y flores pequeñas (alrededor de 1.5 cm de largo en comparación con las de *Oncidium ornithorhynchum* que miden alrededor de 2 cm de largo). Por su parte, *Oncidium pyramidale* tiene la inflorescencia en forma “piramidal” y el callo del labelo y las alas de la columna coinciden con las del dibujo de la obra de Kunth. Por lo tanto, hemos llegado a la conclusión de que el verdadero *Oncidium*

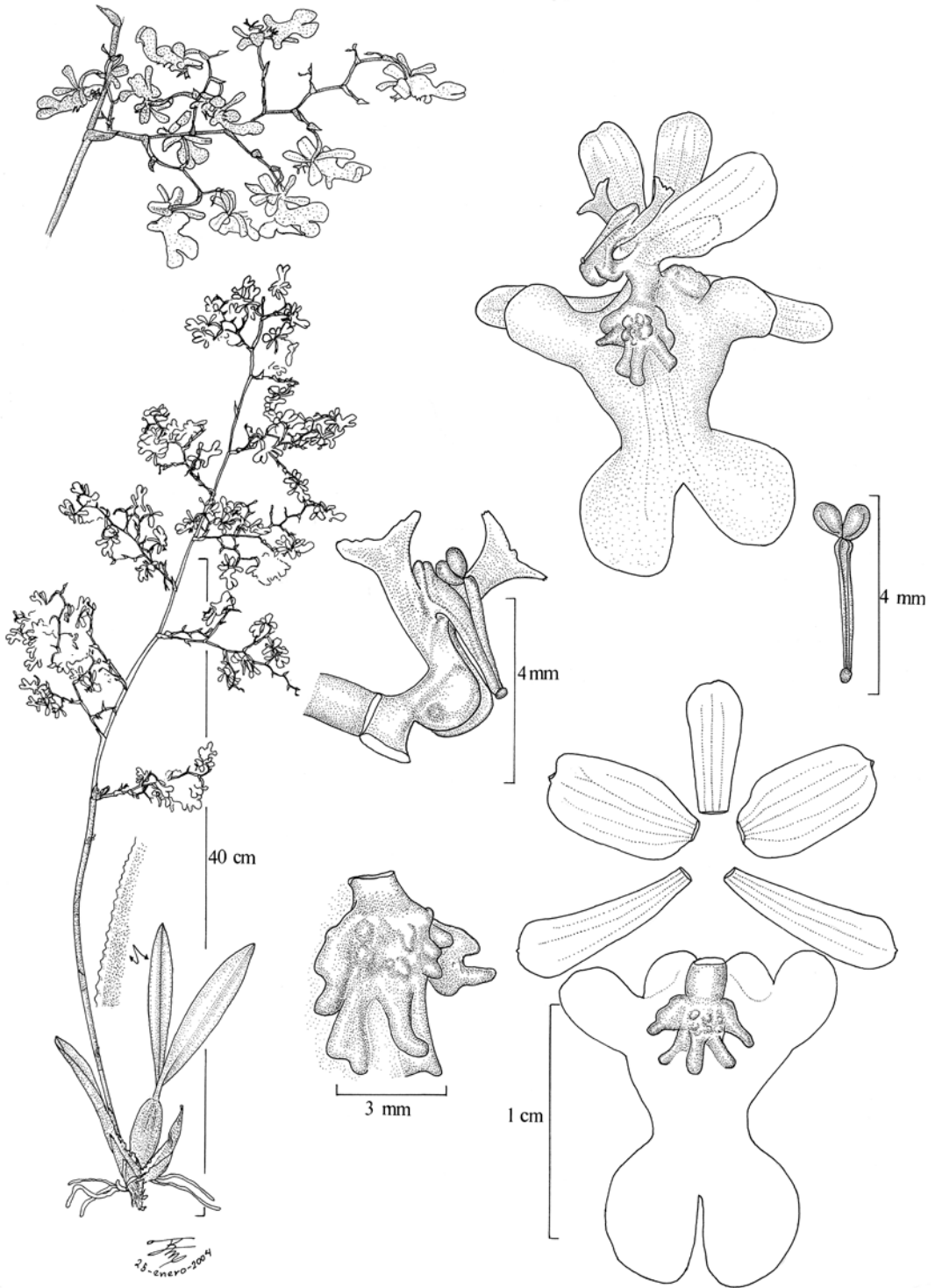


FIGURA 3. Dibujo de *Oncidium ornithorhynchum* Kunth, basado en *Evans, Shultes & Jaramillo 3211*, Colombia, Cundinamarca (AMES). Dibujo de R. Jiménez M.

ornithorhynchum es lo que conocemos como *O. pyramidale* Lindl. de Ecuador, Colombia y Perú. En consecuencia se reduce *O. pyramidale* a sinónimo del primero.

Oncidium ornithorhynchum Kunth, Nov. Gen. & Sp. Pl. 1: 345, t. 80. 1815.

TIPO: América Ecuatorialis, *Humboldt s.n.* (Holotipo: P); Kunth refiere el origen como “*Crescit in temperatis Regni Mexicani prope El Puerto Andaracuas, inter urbes Guanaxuato et Valladolid de Mechoacan, alt. 1010 hex. Floret Septembris*”.

SINÓNIMO: *Oncidium pyramidale* Lindl., Ann. & Mag. Nat. Hist. 15: 384. 1845. TIPO: COLOMBIA. Pasto: *Hartweg s.n.* (Holotipo: K-L! Probable isotipo: *Hartweg s.n.* (ex herbario Lindleyano, W-R 47588, microficha!).

Las plantas son epífitas de los páramos, de los 2850 a los 3340 m de altitud. Florecen en enero. *Oncidium ornithorhynchum* se reconoce por la inflorescencia erecta, en forma “piramidal”, con 90-100 flores; los sépalos espatulados, la columna reflexa con las alas erectas, angostamente cuneadas, con el ápice bilobado (Fig. 3). Es probable que Humboldt y Bonpland hayan colectado el *Oncidium ornithorhynchum* en su viaje a Sudamérica y posteriormente con el transporte de las plantas hubo una confusión en la localidad. No hemos encontrado ningún registro de una colecta de Humboldt y Bonpland de la especie de flores rosadas que tenemos en México y Centroamérica.

ESPECÍMEN EXAMINADO. COLOMBIA. Cundinamarca: Páramo de Guasca, 2850-3340 m, *R. Evans, Shultes & Jaramillo 3211* (AMES!, testigo de ilustración).

Se ha mencionado en la literatura a *O. chrysopyramis* Rehb.f. como sinónimo de *O. pyramidale*, pero esta es una especie diferente distinguiéndose por la inflorescencia más laxa, no en forma “piramidal”, flores de menor tamaño y las alas más angostas y bifidas. Por lo anteriormente expuesto, proponemos a la especie de flores rosadas que se distribuye en México y Centroamérica como nueva:

Oncidium sotoanum R. Jiménez & Hágsater, *sp. nov.*

TIPO: MÉXICO. Veracruz: Orizaba, Cerro San Cristóbal, al sur de Orizaba, a 500 m de la carretera que va a

Córdoba, 1450 m, bosque mesófilo de montaña, con *Lemboglossum [Rhynchosstele] bictoniense* y *Encyclia [Prosthechea] vitellina*, epífita, flores rosadas con callo amarillo-naranja, aroma intenso agradable, dulce, col. 16 abr 1987, prep. mat. cult. 23 oct 1990, *R. Jiménez 626* (Holotipo: AMO, isotipos: K-L, MO, clonotipos: prep. mat. cult. 31 octubre 1987, F; prep. mat. cult. 31 oct. 1989, AMES).

Species *Oncidio ornithorhyncho* Kunth similis, floribus roseis, inflorescentiae arcuatae pendulae architecturae non pyramidalis, alis columnae parallelibus corpo columnae, callo labelli distincto recedit.

SINÓNIMOS: *Oncidium ornithorhynchum* Auct., non Kunth.

Oncidium ornithorhynchum var. *albiflorum* Rehb.f., Gard. Chron. 1873: 503. 1873. TIPO: inflorescencia enviada a H. G. Reichenbach por *Day*, (W-R, no visto).

Hierba epífita, 25-50 cm de alto sin incluir la inflorescencia. *Raíces* delgadas, 0.5-1.2 mm de grosor. *Rizoma* corto. *Seudobulbos* agregados, ovoide-elipsoides, comprimidos, generalmente bifoliados, ocasionalmente trifoliados, lisos, sin costillas, con arrugas longitudinales con la edad, frecuentemente con un canal o surco lateral a ambos lados; verde-glaucos, ásperos, 4-9 x 2.0-3.5 cm; cubiertos en la base por 4-5 vainas subcoriáceas, verde-claras, con margen eroso escarioso inconspicuo (ocupando lo escarioso 1 mm de ancho), 3.5-9.0 cm de largo, las dos superiores foliosas, con lámina foliar articulada, semejante a las hojas 28-45 x 1.5-3.2 cm. *Hojas* 2-3 en el ápice delseudobulbo, erecto-arqueadas, linear-elípticas a lanceoladas u oblanceoladas, largamente acuminadas, subcoriáceas, verde-claras, 16-45 x 1.5-3.3 cm. *Inflorescencia* originada en la base delseudobulbo, aparece cuando el brote nuevo está en desarrollo, floreciendo en el momento en que elseudobulbo madura, 2 a 3 porseudobulbo, raramente 4, paniculada, con ramificaciones secundarias, arqueado-colgante, 30-60 cm de largo, densiflora a congestionada, 45-145 o más flores simultáneas, con pedúnculo de 9-19 cm de largo, verde a ligeramente rojizo; raquis en zigzag; provista de brácteas ovado triangulares, herbáceas, membranáceas, amplexicaules, las del pedúnculo tubulares en la base, de 10-17 mm de largo, las de

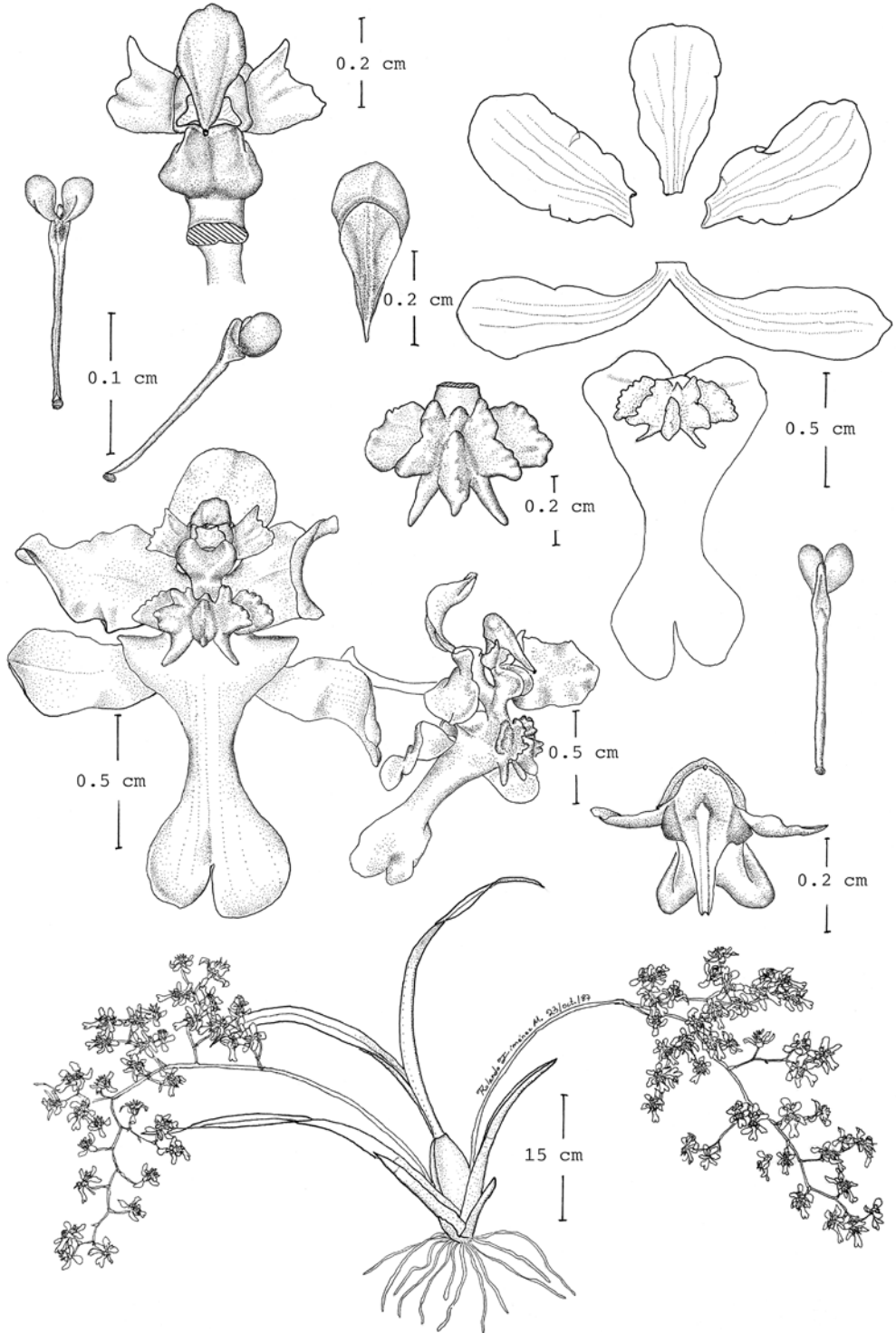


FIGURA 4. *Oncidium sotoanum* R.Jiménez & Hágsater. Basado en R. Jiménez 626, Orizaba, Veracruz, México, AMO (ilustración tomada de Icon. Orchid. (Mexico). 1: pl. 77).



FIGURA 5. Foto de *Oncidium sotoanum* R.Jiménez & Hágsater; *M. A. Soto 4900*, Chiapas, México. Foto de R. Jiménez M.

la base de las ramas no tubulares; agudas, de 3-6 x 3-5 mm. *Brácteas florales* cuculadas, triangulares a ovadas, herbáceo-membranáceas, amplexicaulas, agudas, 1.5-4.0 x 2.5-4.0 mm. *Ovario* pedicelado, tenuemente sulcado, 7-9 mm de largo, 0.8-1.0 mm de grosor. *Flores* vistosas, 16-18 mm de diámetro, sépalos y pétalos rosados, labelo rosado más intenso en la parte basal con los lóbulos laterales blancos, callo amarillo-anaranjado, columna blanca con el ápice rosado, tábula infraestigmática blanca, alas rosadas, antera guinda o intensamente rosada; fragancia intensa, dulce, diurna. *Sépalos* unguiculados a atenuados, obtusos a redondeados, carinados dorsalmente, el *dorsal* reflexo, con la porción apical incurvada, uña de 1 mm de largo; oblanceolado a obovado o elíptico, márgenes deflexos y ligeramente ondulados, trinervado, 6-9 x 2.0-4.5 mm; los *laterales* ligeramente incurvados a extendidos, falcados, brevemente connados en la base, uña de 2 mm de largo; oblanceolado-elípticos, trinervados a 5-nervados, 8.0-11.5 x 2.0-3.5 mm. *Pétalos* incurvados a extendidos, oblicuos, cortamente

unguiculados, uña de 1 mm de largo; ovado elípticos a obovado elípticos o únicamente elípticos, obtusos, con márgenes ondulados, carinados dorsalmente, 5-nervados, 6-10 x 3-5 mm. *Labelo* reflexo, pandurado, trilobado, plano, con la base cordiforme, formando un ángulo de 225° con respecto a la columna, 12-18 x 6-9 mm de ancho entre los lóbulos laterales; éstos semiorbiculares con la porción basal reflexa, la cual envuelve la base de los sépalos laterales para formar un pliegue que secreta un líquido oleaginoso, 3 x 4-7 mm; istmo alargado, angosto, con márgenes deflexos, de 2-3 mm de ancho; lóbulo medio obovado a obcordado, ápice hendido, bilobulado, márgenes enteros, 5-7 x 4-7 mm de ancho; callo prominente, ocupando un cuarto de la longitud total del labelo, formado por 5 quillas lateralmente aplanadas, con el borde eroso, dos cortas hacia los extremos, dos laterales hacia el interior que rematan en el ápice en un cuerno alargado agudo y una central que termina antes de los cuernos alargados agudos, 3.0-3.7 x 4.5-5.2 mm. *Columna* delgada, más ancha en la base que en el ápice, 4-7 mm de largo, alada, con tabula infraestigmática ensanchada en la parte basal, sulcada; alas delgadas, subcuadradas u oblicuamente dolabriformes, margen sinuoso a eroso, paralelas a la columna, 1-2 x 2.0-2.5 mm; rostelo alargado, angostamente triangular; cavidad estigmática subtriangular a subcuadrada, truncada, cóncava, brillante, blanca; clinandrio ovado, guinda o rosa intenso, con una raya blanca que va desde el ápice hasta la parte media. *Antera* claviforme, bilocular, ápice largamente acuminado, 3.5-4.0 x 1.5-2.0 mm. *Polinario* de 3.5 mm de largo, formado por dos polinios sulcados, elíptico obovoides, 0.7 x 0.5 mm; con estípite tubular, 2.3 mm de largo, muy alargado, que termina en una lámina triangular por la cual se sostienen los polinios por medio de las caudículas cortas; viscidio muy pequeño, elipsoide, pardo. *Cápsula* elipsoide a obovoide, redonda en corte transversal, lisa, 1.3 x 1.1 cm, pedicelo 1 cm de largo (Fig. 4 y 5).

ETIMOLOGÍA: Dedicamos esta especie a nuestro colaborador y maestro, recientemente fallecido, Miguel Ángel Soto Arenas, por su dedicación al conocimiento de la biodiversidad, particularmente de las orquídeas, por haber compartido sus conocimientos en salidas al campo y discusiones.

Se distribuye en México, en la parte oriental del Eje Volcánico Transversal, Sierra Madre Oriental, Macizo Central de Chiapas y Sierra Madre de Chiapas en los estados de Veracruz, Tabasco, Oaxaca y Chiapas. Se ha registrado para Centroamérica en Guatemala, El Salvador, Nicaragua y Costa Rica.

Las plantas son epifitas en selva baja o mediana perennifolia, bosque caducifolio, bosque húmedo de encino y ocasionalmente en selva mediana subperennifolia (Montane rain-forest, Oak-pine-*Liquidambar* forest y Evergreen seasonal forest [Breedlove, 1981]), son bosques cálido templados con bastante humedad ambiente durante todo el año; crece a 890-1700 m de elevación. Florece de octubre a febrero, con la mayor floración en noviembre.

Se reconoce por sus pseudobulbos casi glaucos, sin costillas, por las inflorescencias congestionadas, arqueado-colgantes, las flores pequeñas, muy aromáticas, aroma dulce, rosadas, siendo una de las pocas especies de éste género que presentan el color rosado, con el callo amarillo y por el rostelo alargado parecido al pico de un ave. Las plantas no se confunden con ninguna otra especie mexicana, pero las flores por el color rosado se pueden confundir con *Oncidium iricolor* Rchb.f. (sin.: *O. pollardii* Dodson & Hágsater) que tiene las flores rosadas con manchas y puntos morados o magenta, el labelo rosado, la base amarilla, con dos manchas anaranjado-rosadas en el disco a ambos lados del callo y manchas o puntos morados en toda la superficie.

Si bien se trata de una especie que por ahora no está amenazada, algunas poblaciones han disminuido o desaparecido debido a la destrucción intensiva de su hábitat por actividades humanas. Está sujeta a una fuerte presión de colecta, especialmente en el Estado de Veracruz. Es muy apreciada en horticultura por sus plantas compactas con inflorescencias atractivas, densas y numerosas, con flores de color rosado, intensamente aromáticas.

Existen individuos albinos, muy raros, dentro de las poblaciones de *Oncidium sotoanum*, en uno de estos se basó H. G. Reichenbach para describir *Oncidium ornithorhynchum* var. *albiflorum* en el siglo antepasado. Los colores pálidos son raros pero éstos no son los más atractivos; los más vistosos son los colores más oscuros que dan un buen contraste entre el callo amarillo y el labelo.

ESPECÍMENES: MÉXICO. Sin localidad: 1905, *C.A. Purpus 44*, (W-R, diapositiva AMO!); "Presented by Messrs. F. Sander & Co. Albans. 1890" (K-L, diapositiva AMO!); Nov 1886, *H. Veitch s.n.* (K-L, diapositiva AMO!). **Veracruz:** Orizaba, Escamela, 30 sept 1865-1866, *E. Bourgeau 3234* (NY, Px2, BRx2, K-L, diapositivas AMO!); Zacuapam, oct 1938, *J. Linden 195* (K-L, diapositiva AMO!); sin localidad precisa, *S. Rosillo de V. 99* (AMO!). **Tabasco:** Teapa, en el Río Puyacatengo del cruce-UACH, 6 may 1988, *A. Guadarrama et al. 1018* (MEXU!). **Oaxaca:** Sin localidad precisa, 1840, *H. Galeotti 5019* (P, K-L, BRx3, diapositivas AMO!); km 70 de la carretera Oaxaca-Tuxtepec, después de La Esperanza rumbo a Tuxtepec, 1260 m, 13 nov 1987, *R. Jiménez 792 et al.* (AMO!); *ibid.*, prep. mat. cult. 10 nov 1992, *R. Jiménez M. 795 et al.* (AMO!); *ibid.*, prep. mat. cult. 10 ago 1990, (AMOX2!); Sierra San Pedro Nolasco, Talea, 1843-4, *C. Jürgensen 644* (BM, diapositiva AMO!); Ixtlán entre Puerto Eligio a Comaltepec, km 148 entre Tuxtepec y Comaltepec, 26 oct 1965, *G. Martínez-Calderón 436* (MEXUx2!); *ibid.*, km 149, 16 nov 1965, *G. Martínez-Calderón 503* (MEXUx2!); San Miguel Chimalapa, montaña al N de cerro de la División, cerca de 5 km al E de Benito Juárez, cerca de la frontera con Chiapas, cerca de 41 km en línea recta al NNE de San Pedro Tapanatepec, 10 nov 1984, *S. Maya 881* (MEXU!); *ibid.*, arroyo El Caracol, parte inferior, al O de Benito Juárez, cerca de 39-40 km en línea recta al N de Tapanatepec, 15 nov 1984, *S. Maya 912* (MEXU!); San Miguel Chimalapa, Filo de la Culebra, entre Cerro Guayabito y Cerro Salomón, ca. 7 km en línea recta al NW de Benito Juárez, ca. 42 km en línea recta al N de San Pedro Tapanatepec, 25 nov 1985, *S. Maya 2571* (CHAPA!); San José Tenango, Teotitlán Cañada, camino de San Martín Caballero a Tenango, a 3 km de San Martín, 1500 m, 26 oct 1992, *S. Salas 335* (AMO!); Santa María, al pie de la vertiente N de la Sierra de Tres Picos, 1 abr 1996, *G.A. Salazar 5526* (AMO!); camino Oaxaca-Tuxtepec km 114, 4500', oct 1977, *Thurston 1739 sub E. Hágsater 5436* (AMO!). **Chiapas:** Camino Palenque Ocosingo, km 15, prep. mat. cult. 24 dic 1976, *E. Hágsater 2359* (AMOX3!); Las Margaritas, a 12 km al E de Lago Tziscoa camino a Ixcán, 1250 m, 16 nov 1984, *E. Martínez 8631* (AMO!); monte Ovando, 14 nov 1939, *E. Matuda 4019* (MEXUx2!); Lagos de Montebello, *M. Rodríguez s.n.*, (AMO!); ca. km 3 del camino de Tziscoa-Márquez de

Comillas, cerca de los límites del Parque Lagunas de Montebello, 13 oct 1985, *M.A. Soto 1644 et al.* (AMO!); Ocosingo, alrededores de la Laguna Ocotilito entre Mezabok y Monte Libano, 950 m, 16 jun 1986, *M.A. Soto & E. Martínez 2691* (AMOX3!); 500 m debajo de Rayón, 1340 m, 10 abr 1989, *M.A. Soto & E. Martínez 4900* (AMO!); Las Margaritas, ca. de Nuevo Momón, 41.28 km al E de Las Margaritas, por el camino a Cruz del Rosario, 1500-1600 m, 9 ago 1992, *M.A. Soto & R. Solano 7163* (AMO!); La Independencia, km 41.7 del camino Montebello-Márquez de Comillas, 17 jul 1999, *M.A. Soto & L. López 9040* (AMOX3!); Union Juárez, 16 nov 1985, *E. Ventura & López 2733* (ENCB!); between Cañada Honda (300 m) to El Triunfo (2100 m), along southern slopes Sierra de Soconusco to crest, 6 Nov 1945, *E.H. Xolocotzi & A.J. Scharp 364* (MEXUX3!). EL SALVADOR: sin localidad, prep. mat. cult. 4 dic 1998, *E. Salaverría* sub *E. Hágsater 7845* (AMOX2!); *Ibid.*, prep. mat. cult. 24 nov 2000, (AMO!).

OTROS REGISTROS: MÉXICO. Veracruz: Orizaba, nov 1931, florecida en cultivo 30 nov 1932, *O. Nagel sub Oestlund 1761* (dibujos y datos [notas E. Oestlund] AMO!).

En los estados de Oaxaca y Chiapas, existe una población de *Oncidium sotoanum* que difiere en el tamaño de la planta, el aroma de las flores y detalles del callo, la cual se propone a continuación como nueva subespecie. Por sus plantas de porte pequeño con inflorescencias cortas, se podría usar como novedad para el cultivo.

Oncidium sotoanum R.Jiménez & Hágsater ssp. ***papalosomeum*** R.Jiménez, ssp. nov.

TIPO: MÉXICO. Oaxaca: km 178 del camino Oaxaca-Pto. Escondido, “Río salado”, 1350 m. Pinar de *Pinus oocarpa* con bosque mesófilo-selva mediana en las cañadas, muy húmedo, con cafetales, con *Restrepia xanthophthalma* [*muscifera*], *Mexicoa* [*Oncidium*] *ghiesbregtiana*, *Trichocentrum hoegii*, *Trichosalpinx blaisdelli* y *Oncidium karwinskii*, epítita. Tépalos lila oscuro, labelo lila pálido, callo amarillo intenso, aroma dulce, intenso (tarde). Escaso en la localidad, plantas excepcionalmente pequeñas para la especie, 17 noviembre 1987, prep. mat. cult. 10 ago 1990, *M.A. Soto 3923*, *R. Jiménez & F. Rodríguez*. (Holotipo:

AMO, Isotipo: AMES; testigo de ilustración).

Formae typicae similis, plantis minoribus, inflorescentiis brevis pauciramosis, aromae floribus Phorophyllo (vulgo dictus Pápalo) affinis, callo compacto recedit. In clivis Oceani Pacifici agrorum Mexicanorum Oaxacensis et Chiapasensis distributa.

Hierba epífita, 17-20 cm de alto sin incluir la inflorescencia. *Raíces* delgadas, 0.5-1.0 mm de grosor. *Rizoma* corto. *Seudobulbos* agregados, ovoide-elipsoides, comprimidos, bifoliados, lisos, sin costillas, con arrugas longitudinales con la edad, frecuentemente con un canal o surco lateral a ambos lados; verde-glaucos, ásperos, 3.0-6.5 x 1-3 cm; cubiertos en la base por 3-5 vainas subcoriáceas, verde-claras, con margen eroso-escarioso inconspicuo, 1.5-4.5 cm de largo, las dos o tres superiores foliosas, con lámina foliar articulada, semejante a las hojas, 4-22 x 0.8-3.0 cm. *Hojas* 2 en el ápice delseudobulbo, erecto arqueadas, linear elípticas a lanceoladas, acuminadas, subcoriáceas, verde-claras, 9-26 x 1.0-2.8 cm. *Inflorescencia* originada en la base delseudobulbo, aparece cuando el brote nuevo está en desarrollo, floreciendo en el momento en que elseudobulbo madura, 1 a 2 porseudobulbo, paniculada, erecto-arqueada, 10-30 cm de largo, densiflora, 10-20 flores simultáneas, con pedúnculo de 4-6 cm de largo, ligeramente flexuoso; ramas fuertemente en zig-zag; provista de brácteas ovado triangulares, herbáceas, membranáceas, amplexicaules, las del pedúnculo tubulares en la base, 0.6-1.3 mm de largo, las de la base de las ramas no tubulares, agudas, 6 x 3 mm. *Brácteas florales* cuculadas, triangulares a ovadas, herbáceo-membranosas, amplexicaulas, agudas, 2 x 4 mm. *Ovario* pedicelado, tenuemente sulcado, 7-17 mm de largo, 0.5-1.0 mm de grosor. *Flores* vistosas, 16-27 mm de diámetro, sépalos y pétalos rosados, labelo rosado, magenta-oscuro intenso en la base, con lóbulos laterales blancos, callo amarillo, manchado de anaranjado, columna blanca con el ápice rosado, tabula infraestigmática blanca, alas rosadas, antera guinda o intensamente rosada; fragancia intensa, dulce, a Pápalo (hierba del género *Phorophyllum*), diurna. *Sépalos* unguiculados, obtusos a redondeados, carinados dorsalmente, 5-nervados, el *dorsal* reflexo, con la porción apical recurvada, uña de 1-2 mm de largo; oblanceolado a obovado, márgenes

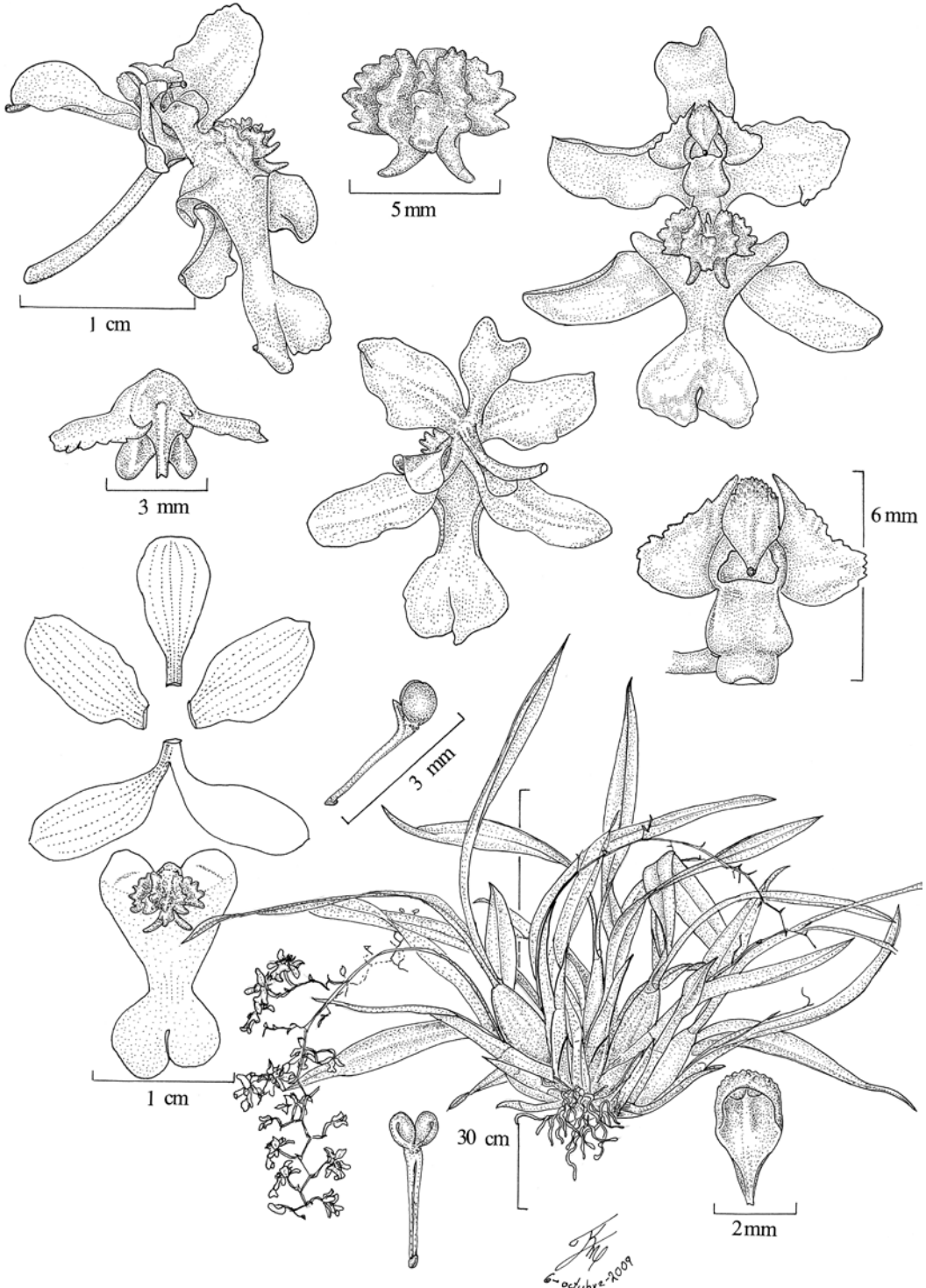


FIGURA 6. *Oncidium sotoanum* R.Jiménez & Hágsater ssp. *papalosum* R.Jiménez, basado en *M.A. Soto 2803*, Chiapas, México. Dibujo de R. Jiménez M.



FIGURA 7. *Oncidium sotoanum* ssp. *papalosmum*, M.A. Soto 2803, Chiapas, México. Foto de R. Jiménez M.

ligeramente ondulados, 5-nervados, 7.5-10.0 x 2.5-5 mm; los *laterales* extendidos, falcados, brevemente connados en la base, uña de 2-3 mm de largo; oblanceolado-elípticos, 5-nervados, 8-12 x 2.5-4 mm. *Pétalos* de incurvados a extendidos, oblicuos, cortamente unguiculados, uña de 1 mm de largo; ovado-elípticos, redondeados, márgenes ondulados, carinados dorsalmente, 5-nervados, 7-10 x 4-5 mm. *Labelo* reflexo, pandurado, trilobado, plano, con la base cordiforme, 13-16 x 5.5-11 mm de ancho entre los lóbulos laterales; éstos semiorbiculares con la porción basal reflexa, la cual envuelve base de los sépalos laterales, y en donde se localiza un pliegue que secreta un líquido aceitoso, 3 x 4 mm; istmo alargado, angosto, con márgenes deflexos, de 3 mm de ancho; lóbulo medio obovado a obcordado, ápice hendido, bilobulado, márgenes enteros, 5-6.5 x 5-6.5 mm; callo prominente, ocupando un tercio de la longitud total del labelo, formado por 5 quillas lateralmente aplanadas, dentadas, dos cortas en los extremos, dos laterales hacia el interior que terminan en el ápice en un cuerno agudo, recurvado y una central baja que termina antes de los cuernos agudos, 3-4 x 3-5 mm. *Columna* delgada, más ancha en la base que en el ápice, delgada, 4-7 mm de largo, alada, con

tabula infraestigmática ensanchada en la parte basal, sulcada; alas delgadas, semiovasdas o dolabriformes, margen sinuoso a eroso, paralelas a la columna, 1-2 x 2-2.5 mm; rostelo alargado, angostamente triangular; cavidad estigmática subtriangular truncada, cóncava, brillante, blanca; clinandrio ovado, color guinda o rosa intenso, con una raya blanca que va desde el ápice hasta la parte media. *Antera* claviforme, bilocular, ápice largamente acuminado, papilosa, 3.5-4 x 1.5-2 mm. *Polinario* de 3-3.5 mm de largo, formado por dos polinios sulcados, elíptico obovoides, 0.7 x 0.5 mm; con estípite tubular, 2.3-2.8 mm de largo, muy alargado, que termina en una lámina triangular, por la cual se sostienen los polinios, por medio de las caudículas cortas; viscidio muy pequeño, elipsoide, pardo. *Cápsula* no vista (Fig. 6 y 7).

ETIMOLOGÍA. El nombre “*papalosmum*” proviene del Nahuatl *papaloquilitl* (plantas del género *Phorophyllum*) y -οσμη, del Griego, que huele, se refiere al olor de esta planta muy usada en la cocina tradicional y conocida coloquialmente como “Pápalo”.

Se distribuye en las laderas de la Sierra Madre del Sur y la Sierra Madre de Chiapas en su vertiente orientada hacia el Océano Pacífico en los estados de Oaxaca y Chiapas. Crece epífita en barrancas húmedas con bosque mesófilo, a 950-1400 m de elevación. Florece de agosto a diciembre.

Se reconoce por las plantas pequeñas de 17-20 cm de alto, por las inflorescencias cortas de 10-30 cm de largo, con ramas fuertemente en zig-zag; por las flores rosadas con el labelo magenta-oscuro intenso en la base; por el aroma herbáceo, parecido a una planta de la familia de las Compuestas del género *Phorophyllum*, la cual es comestible y en México recibe el nombre común de “Papaloquelite” o “Pápalo”, muy distinto al aroma dulce intenso de la especie; por las alas de la columna semiovasdas o dolabriformes y por su distribución en las laderas orientadas al Océano Pacífico, en los estados de Oaxaca y Chiapas.

OTROS ESPECÍMENES. **MÉXICO. Oaxaca:** Entre Finca Copalita y Pluma Hidalgo, 950-1100 m, 11 may 1994, M.A. Soto 7617 et al. (AMO!). **Chiapas:** Jiquipilas, Cerro La Palmita, 1340 m, 7 nov 1994, J. J. Castillo et al. 403 (AMO!); sin localidad precisa, prep. mat. cult.

21 oct 1981, *E. Hágsater 536* (AMO!); Mapastepec, Reserva El Triunfo, 1200 m, 25 XI 1989, *M. Heath & A. Long 323* (AMO!); Parte media del Cerro Tres Picos, ladera norte, al SE de Villa Flores, 1300 m, 10 VI 1986, *M.A. Soto 2803 et al.* (AMO!, testigo de ilustración); Cerro Tres Picos, 47-48 km de la desviación Cintalapa-Arriaga, ca. 1200 m, 13 VII 1989, prep. mat. cult. 23 dic 1987, *M.A. Soto 3193 et al.* (AMO!).

AGRADECIMIENTOS. Deseamos agradecer al Dr. Gustavo

Romero del herbario AMES, por el préstamo de material de *Oncidium pyramidale* y la información amablemente proporcionada sobre la obra de Kunth. Al Dr. Adolfo Espejo Serna del herbario UAMIZ por habernos proporcionado la imagen del tipo de *O. ornithorhynchum* del herbario de Paris (P). A Astrid H. de Restrepo de la Sociedad Colombiana de Orquideología por la imagen de *O. pyramidale*. Al Dr. Rodolfo Solano del CIIDIR-Oaxaca, la revisión crítica del manuscrito y sus valiosas sugerencias. A Franco Pupulin por las diagnósis latinas.

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TWO NEW SPECIES OF *LEPANTHES* FROM COSTA RICA CLOSE TO *L. SCHIZOCARDIA* (ORCHIDACEAE: PLEUROTHALLIDINAE)

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ABSTRACT. We revise the group of species close to *Lepanthes schizocardia*, and we describe and illustrate two new species from Costa Rica. *Lepanthes montis-narae* is compared with the Panamanian *L. schizocardia*, from which it mainly differs by the pendent plants, the dark gray green leaves, the ovate to orbicular, subacuminate leaves, the inflorescences borne above the leaf, the petals with inequal lobes, the apical lobe ovate, acute, the lower lobe smaller than the upper lobe, narrowly ovate, the scarlet lip and the conic, apically ciliate appendix. *Lepanthes sotoana* is similar to *L. maxillaris* from Ecuador. It can be distinguished by the pendent plants, the dark gray green leaves, the inflorescences borne above the leaf, the acute lateral sepals, the lip with subfalcate lateral lobes touching each other and hiding the base of the appendix. We also illustrate for the first time *L. schizocardia* to facilitate species comparison.

RESUMEN. Revisamos el grupo de especies cercanas a *Lepanthes schizocardia* y describimos e ilustramos dos nuevas especies de Costa Rica. *Lepanthes montis-narae* es comparada con la panameña *L. schizocardia*, de la cual se diferencia principalmente por las plantas pendulosas, las hojas verde oscuro grisáceas, las hojas ovadas a orbiculares, subacuminadas, las inflorescencias que se desarrollan encima de la hoja, los pétalos con lóbulos desiguales, el lóbulo apical ovado, agudo, el lóbulo inferior más pequeño que el lóbulo superior, ligeramente ovado, el labelo escarlata y el apéndice cónico, apicalmente ciliado. *Lepanthes sotoana* es similar a *L. maxillaris* de Ecuador. Puede ser distinguida por las plantas pendulosas, las hojas verde oscuro grisáceas, las inflorescencias que se desarrollan encima de la hoja, los sépalos laterales agudos, el labelo con lóbulos laterales subfalcados que se tocan el uno al otro y esconden la base del apéndice. También ilustramos por primera vez a *L. schizocardia* para facilitar la comparación de las especies.

KEY WORDS: Orchidaceae, Pleurothallidinae, *Lepanthes montis-narae*, *L. sotoana*, *L. schizocardia*, *L. maxillaris*, new species, Costa Rica

The genus *Lepanthes* Sw. is probably the most diverse in the floras of the Neotropics and one of the largest plant genera in the world, with more than 700 species distributed in the West Indies and from Mexico to Bolivia and Brazil. According to the geographic records, most of the species are very restricted in distribution, often with narrow regional and local endemisms. Besides the inherent difficulty of comparing an unusually large number of taxa, species of *Lepanthes* are mostly easy to identify on the basis of their vegetative and floral features. The generalized morphological scheme of *Lepanthes* flowers (with mostly transversely bilobed petals and

a lip provided with thickened, erect lateral lobes and a minute apical appendix) has impeded until recently to formally recognize fine subgeneric ranks. Even within the grouping proposed by Luer, who divided the genus into subgenera, sections, subsections and series (Luer 1986, 1987a, 1987b, 1993, 1996), most of the taxa are assigned to subgen. *Lepanthes* sect. *Lepanthes* subsect. *Lepanthes* ser. *Lepanthes*. This large group, mostly characterized by a congested raceme with short rachis internodes, is quite homogeneous in floral morphology, but several informal groups of species can be recognized by some peculiar combinations of characters.

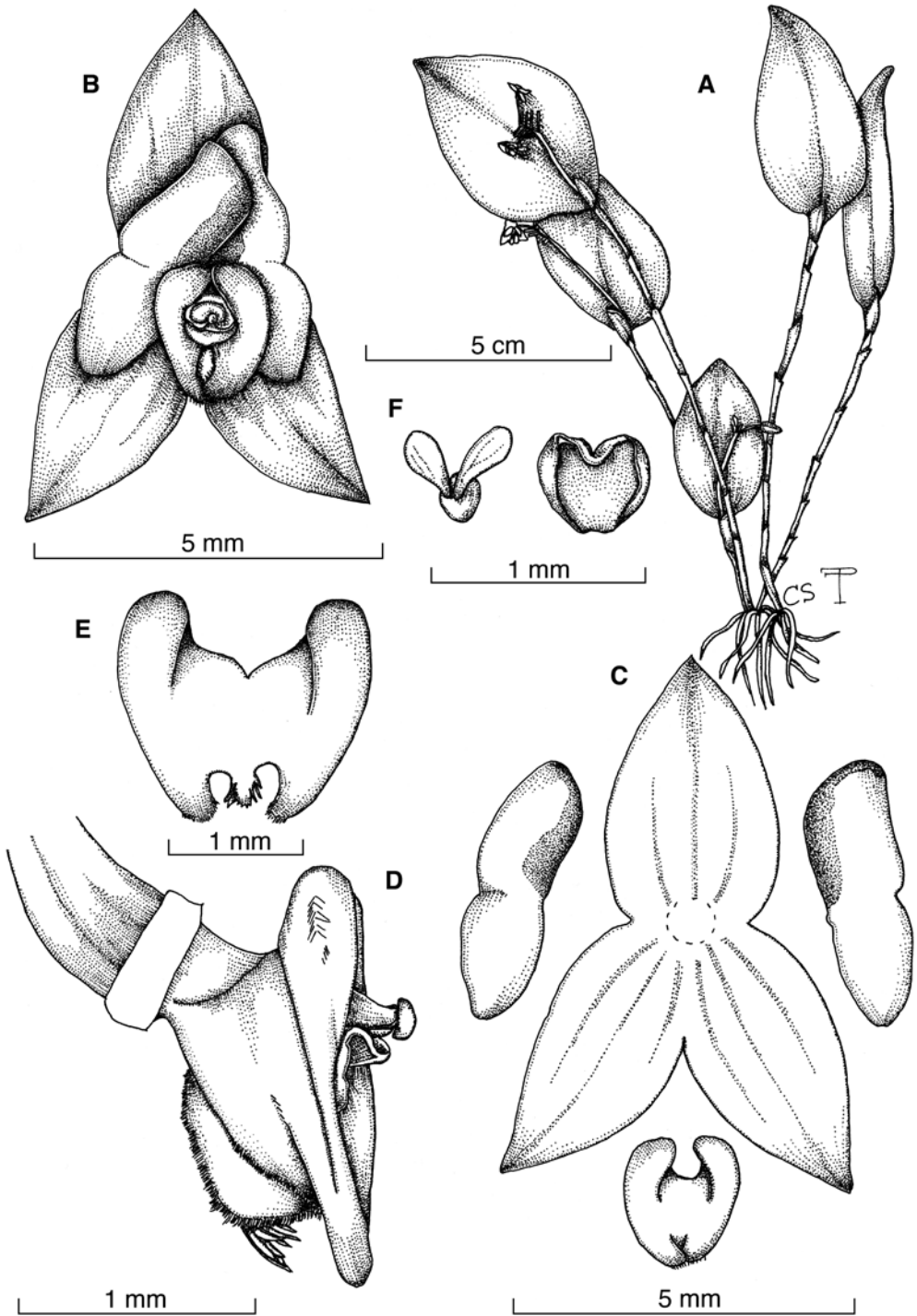


FIGURE 1. *Lepanthes schizocardia* Luer. A — Habit. B — Flower. C — Dissected perianth. D — Ovary, column and lip, lateral view. E — Lip, adaxial view. F — Pollinarium and anther cap. Drawing by F. Pupulin and C. M. Smith based on *D. Bogarín* 5940 (JBL).

TABLE 1: Comparison of characteristics of the different taxa.

Character	<i>L. montis-narae</i>	<i>L. schizocardia</i>	<i>L. sotoana</i>
Habit	pendent	erect	pendent
Leaves	not reticulated ovate to orbicular, subacuminate	reticulated elliptic, acute	not reticulated ovate to orbicular, subacuminate
Inflorescences	borne above the leaf	borne beneath the leaf	borne above the leaf
Apical petal lobe	ovate	oblong	oblong
Lower petal lobe	smaller than upper lobe	equal to upper lobe	equal to upper lobe
Lip lobes	hiding the column	hiding the column	not hiding the column
Apex of lip lobes	touching each other	touching each other	not touching each other
Lip color	scarlet	orange	scarlet
Lip appendix	cylindric, ciliate	oblong, bristly	oblong, ciliate

We refer here to one of these morphological alliances with the name of *Lepanthes schizocardia* group, characterized by a cleft lip with the blades scarcely distinct from the connectives, sometimes mandible-like in shape, and particularly long appendices. Carlyle Luer described the first species of the group, *L. schizocardia*, from Panama (Luer 1984), the specific epithet (“split heart”) alluding to its characteristic, cleft, heart-shaped lip. The species was not illustrated with the protologue (Luer 1984), and we take this opportunity to present here a composite plate based on Panamanian material originally collected at the type locality (Fig. 1, 4). Two closely allied species (*L. maxillaris* Luer & Hirtz and *L. didyma* Luer & Hirtz) were subsequently described from Ecuador (Luer 1996). The group ranges to the North to Costa Rica, where a few collections were previously identified at the herbarium of the University of Costa Rica and in the living collection of Lankester Botanical Garden (LBG) as *L. schizocardia*.

In 2007, researchers at LBG began working to a complete survey of the species of Pleurothallidinae in Costa Rica, eventually intended as a contribution to the *Flora Costaricensis*. In the framework of this project, we are critically revising the identity of the species previous recorded from Costa Rica, comparing specimens from local populations with the original materials and, whenever possible, with living plants of the concerned taxa, preferably from type localities. The importance of transnational floristic projects combined with extensive examination of natural populations in the field cannot be overemphasized. As

orchid populations are many times either found only in a narrow geographical range or in reduced numbers it is essential that studies be carried out over a broad geographical areas in a thorough manner.

In revising Costa Rican materials previously assigned to *L. schizocardia*, we discovered two species that we described here as new to science. The main differences between the three taxa are summarized in Table 1.

Lepanthes montis-narae Pupulin, Bogarín & C. Smith, *sp. nov.*

TYPE: COSTA RICA. San José: Dota, crest of Cerro Nara, 910-1000 m, epiphytic in premontane rain forest, disturbed primary forest, 20 Feb. 2000, *F. Pupulin 2103*, *D. Castelfranco*, *L. Spadari* & *K. McFarland* (holotype: JBL; isotype: USJ). FIG. 2, 4.

A *Lepanthes schizocardia* Luer similis, sed planta pendula, foliis fuscatis viridi-griseus ovatis-orbicularis subacuminatis, inflorescentiis folii portatis abaxialibus, lobulis petalorum inaequalibus, lobo superno ovato acuto, lobo infero minore, anguste ovato, labello scarlatino appendice conica ciliata recedit.

Epiphytic, caespitose, pendent *herb*, up to 14.5 cm tall. *Roots* slender, flexuous, to 1 mm in diameter. *Ramicauls* pendent, up to 10.5 cm long, enclosed by 9 – 11 glabrous, lepanthiform sheaths, the ostia glabrous. *Leaves* coriaceous, dark green, ovate to orbicular, conduplicate, subacuminate, emarginate, with a short apiculus, 3.0–4.0 x 1.4–3.0 cm, the

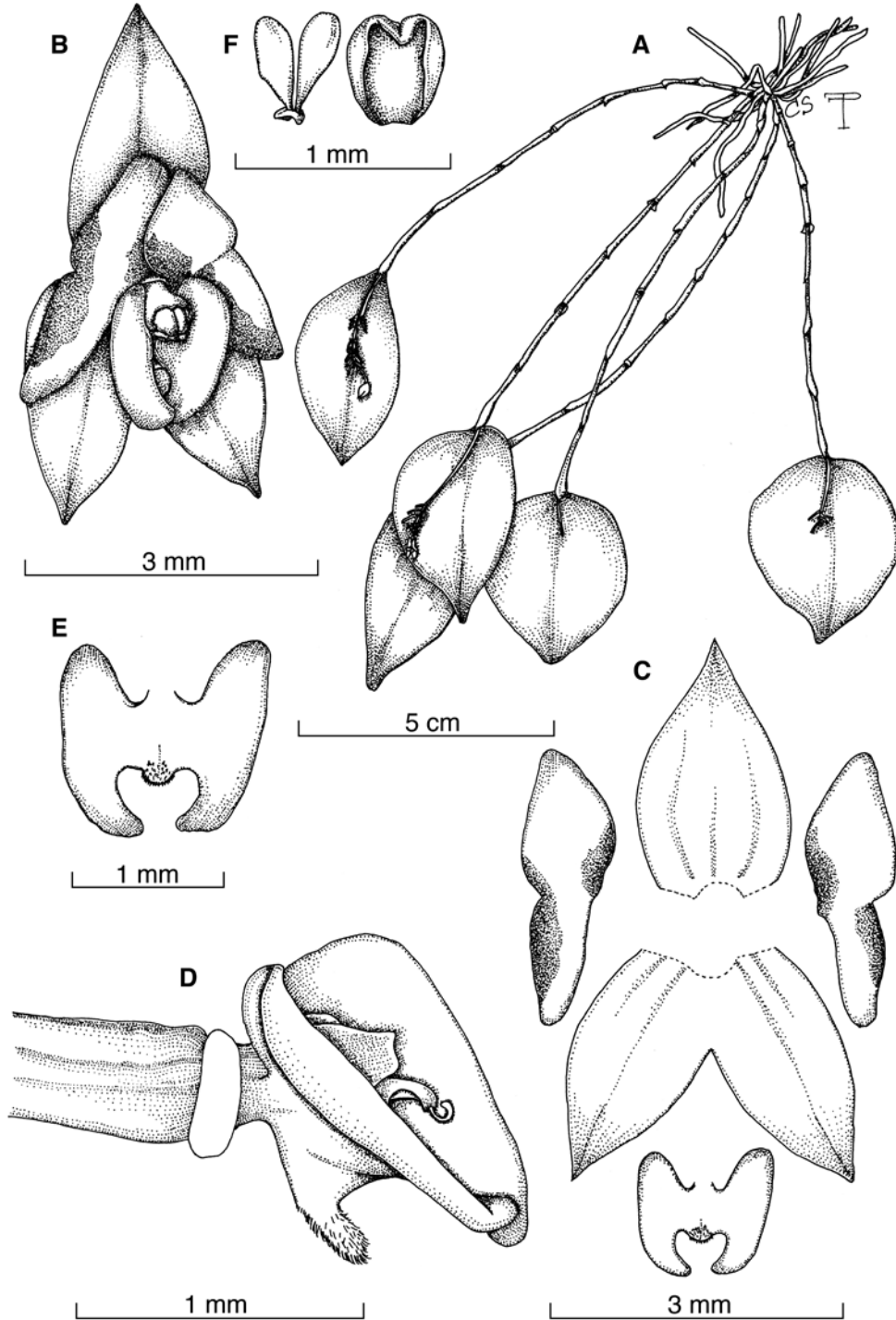


FIGURE 2. *Lepanthes montis-narae* Pupulin, Bogarín & C. Smith. A — Habit. B — Apex of inflorescence. C — Flower, side view. D — Dissected perianth. E — Lip, frontal view. F — Lip, lateral views. G — Petals, lateral views. H — Pollinarium and anther cap. Drawing by F. Pupulin and C. M. Smith from the holotype.

rounded base narrowing into a petiole less than 1 mm long. *Inflorescence* racemose, distichous, glabrous, successively flowered, borne above the leaf, shorter than leaves, up to 2.8 cm long, peduncle 1.1–1.9 cm long, rachis 0.3–1.2 cm long. *Floral bracts* 1 mm long, glabrous. *Pedicels* 2.5–4.0 mm long, persistent. *Ovary* to 2 mm long. *Flowers* orange with red-scarlet, the sepals orange tinged with red, the petals red-scarlet, the lip scarlet. *Dorsal sepal* ovate, acute, connate to the lateral sepals for about 0.4 mm, 3.0 x 1.5 mm. *Lateral sepals* ovate to elliptic, acute, connate for 0.9 mm, 2.6 x 1.2 mm. *Petals* transversely bilobed, entire, 1.1 x 3.1 mm, the upper lobe ovate, obtuse, the lower lobe smaller than the upper lobe, narrowly oblong, the apex rounded. *Lip* bilobate, adnate to the column, the blades oblong with rounded ends and the apex entire, falcate, 1.3 x 0.9 mm, the connectives terete, to 1 mm long, lifting the blades above the column, the body oblong, connate to the base of the column, the appendix small, oblong, pubescent, slightly curved upward. *Column* cylindrical, 0.7 mm long, the anther apical, the stigma ventral. *Pollinia* two, ovoid. *Anther cap* cucullate.

PARATYPE: COSTA RICA. San José: Dota, crest of Cerro Nara, 910–1000 m, epiphytic in premontane rain forest, disturbed primary forest, 20 Feb. 2000, *F. Pupulin 2102*, *D. Castelfranco*, *L. Spadari* & *K. McFarland* (JBL-spirit, USJ!).

DISTRIBUTION: only known from Costa Rica.

HABITAT AND ECOLOGY. The only known specimens were found epiphytic in disturbed primary vegetation in premontane rain forest, between 900 and 1000 m of elevation. Apparently, it is restricted to the crest of Cerro Nara in central Pacific Costa Rica.

ETYMOLOGY: Named after Cerro Nara, the mountain where the type specimen was collected.

Lepanthes montis-narae is most similar to the Panamanian endemic *Lepanthes schizocardia* Luer. It can be distinguished by the pendent plants (vs. erect), the dark gray green leaves (vs. reticulated in purple beneath), ovate to orbicular, subacuminate leaves (vs. elliptic, acute), inflorescences borne above the leaf (vs. beneath the leaf), the petals with unequal lobes (vs. subequal), the apical lobe ovate (vs. oblong), the

lower lobe smaller than the upper lobe, narrowly ovate (vs. as long as the upper lobe, ovate), the scarlet lip (vs. orange) and the conic, apically ciliate appendix of the lip (vs. ovate, apically bristly).

Lepanthes sotoana Pupulin, Bogarín & C. Smith, *sp. nov.*

TYPE: COSTA RICA. San José: Pérez Zeledón, Miraflores, road to Santa Cruz, 1350 m, epiphytic on secondary vegetation and remnants of primary, lower montane rain forest, 2 December 2001, *F. Pupulin 3484*, *D. Castelfranco* & *J. Cambroner* (holotype: JBL; isotypes: CR, JBL). FIG. 3, 4.

A *Lepanthes maxillaris* Luer similis, sed planta pendula, foliis fuscatis viridi-griseis, inflorescentiis folii portatis abaxialibus, sepalis lateralibus acutis, lobis lateralibus labelli subfalcatis apicalibus contiguus, base appendicis occulta.

Epiphytic, caespitose, pendent *herb*, up to 9.3 cm tall. *Roots* slender, flexuous, to 1 mm in diameter. *Ramicauls* slender, pendent, up to 5 cm long, enclosed by 4–8 glabrous, lepanthiform sheaths, the ostia glabrous and non dilated. *Leaves* coriaceous, dark grayish green, lightly suffused with purple beneath, ovate to orbicular, conduplicate, acute, emarginated with a short apiculus, 2.2–4.0 x 1.2–2.6 cm, the rounded base narrowing into a petiole less than 1 mm long. *Inflorescence* racemose, distichous, glabrous, successively flowered, borne above the leaf, up to 1.5 cm, peduncle 0.8–1.2 cm long, rachis 0.3–0.5 cm long. *Floral bracts* 1 mm long, glabrous. *Pedicels* 3–4 mm long, persistent. *Ovary* to 2 mm long. *Flowers* orange with red-scarlet, the sepals orange tinged with red, the petals red-scarlet. *Dorsal sepal* ovate, acute, connate to the lateral sepals for about 0.6 mm, 3.4 x 1.7 mm. *Lateral sepals* ovate, acute, connate for 0.7 mm, 2.8 x 1.4 mm. *Petals* transversely bilobed, entire, 0.8 x 2.7 mm, the upper lobe oblong, obtuse, the lower lobe, oblong to ovate, obtuse. *Lip* bilobate, adnate to the column, the blades oblong with rounded ends and the apex ciliate, subfalcate, 1.5 x 1.3 mm, the connectives terete, to 1 mm long, perpendicular to the column and leaving it exposed, the body oblong, connate to the base of the column, the appendix small, oblong, convex, ciliate, with

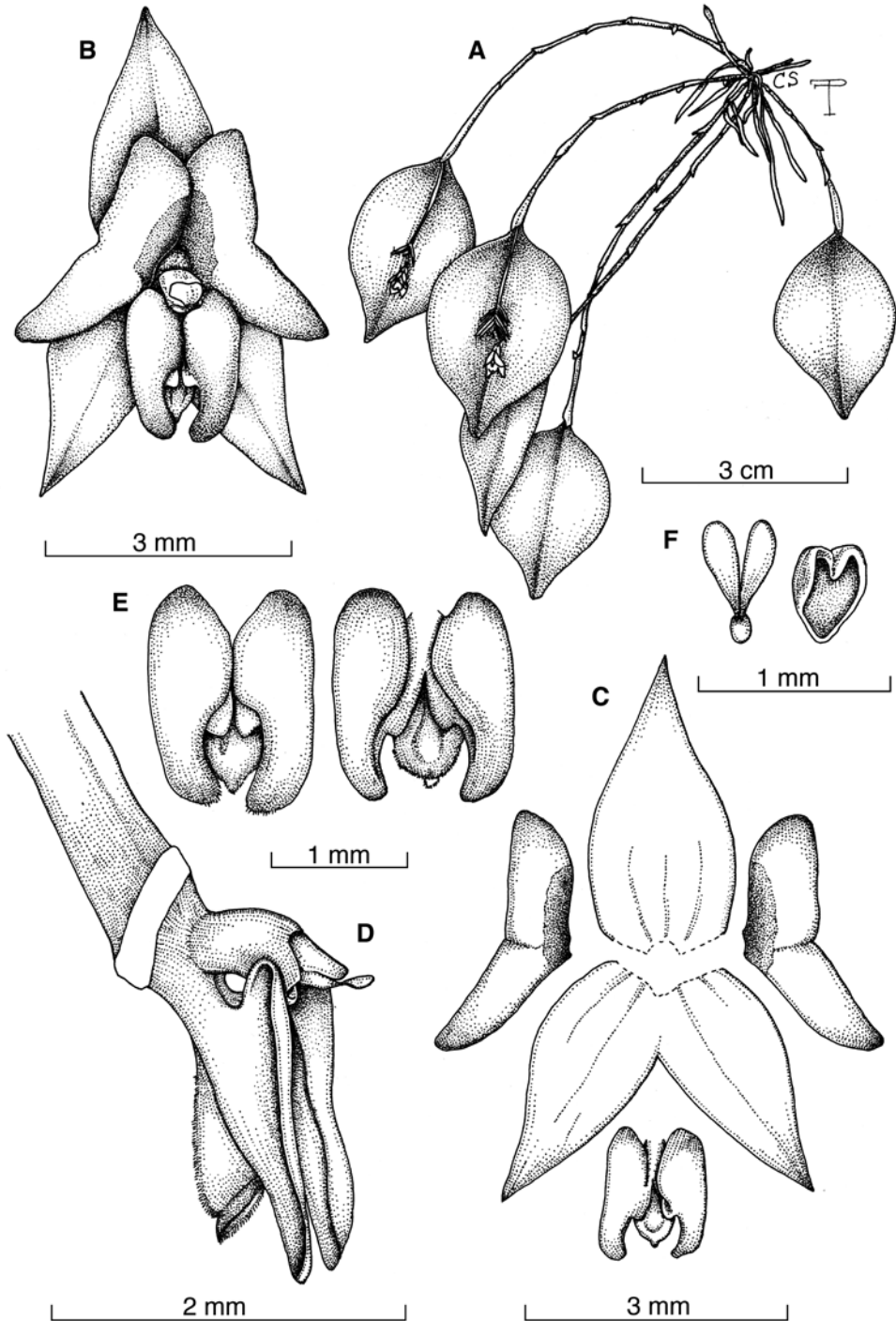


FIGURE 3. *Lepanthes sotoana* Pupulin, Bogarín & C. Smith. A — Habit. B — Apex of inflorescence. C — Flower, side view. D — Dissected perianth. E — Lip, frontal view. F — Lip, lateral views. G — Petals, lateral views. H — Pollinarium and anther cap. Drawing by F. Pupulin and C. M. Smith from the holotype.

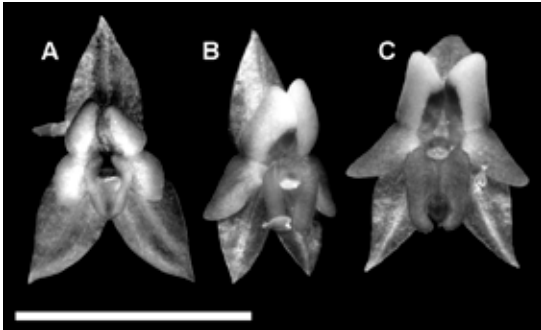


FIGURE 4. *Lepanthes sotoana* Comparison of the flowers of: A — *Lepanthes schizocardia* (Bogarín 5940). B — *L. montis-narae* (Pupulin *et al.* 2103). C — *L. sotoana* (Pupulin *et al.* 3484). Scale bar = 5 mm.

a short apicule. *Column* cylindric, 1 mm long, the anther apical, the stigma ventral. *Pollinia* two, ovoid. *Anther cap* cucullate.

PARATYPES. COSTA RICA. San José: Pérez Zeledón, Berlín, november 1998, collected by G. Chacón Valverde *s.n.*, flowered in cultivation under accession number JBL-00269, 19 september 2002, JBL-00269 (JBL-spirit); Pérez Zeledón, Miraflores, road to Santa Cruz, 1350 m, epiphytic on secondary vegetation and remnants of primary, lower montane rain forest, 2 December 2001, F. Pupulin 3483, D. Castelfranco & J. Cambronero (JBL-spirit); Pérez Zeledón, Las Nubes de Quizarrá, collected by N. Fonseca, flowered in cultivation at San Isidro del General, 2 May 2000, F. Pupulin 2319 (USJ).

DISTRIBUTION: only known from Costa Rica.

HABITAT AND ECOLOGY: Plants of this species are found in tropical wet forest, tropical moist forest, premontane belt transition and premontane rain forest, between 800 and 1400 m of elevation. The species is apparently restricted to the El General Valley in San Isidro de Pérez Zeledón, in the Pacific slope of Talamanca range in Costa Rica.

Eponymy: The specific epithet honors the memory of the late Miguel Ángel Soto Arenas, a Mexican orchidologist who made great contributions to the knowledge of the family in the Neotropics.

Lepanthes sotoana is closely related to *Lepanthes maxillaris* Luer from Ecuador. It can be distinguished

by the pendent plants (*vs.* erect), the dark gray green leaves (*vs.* reticulated in purple beneath), the inflorescences borne above the leaf (*vs.* beneath the leaf), the acute lateral sepals (*vs.* acuminate), the lip with subfalcate lateral lobes touching each other, hiding the base of the appendix (*vs.* falcate, separated, leaving exposed the appendix).

Lepanthes montis-narae and *L. sotoana* had been collected and cultivated at Lankester Botanical Garden since several years. The habit and flowers of both species are superficially similar, resembling those of *L. schizocardia*. After studying the type of *L. schizocardia*, we found both species consistently different. The plants are pendent, lacking the purple reticulation beneath the leaves and the inflorescences borne above the leaf. *Lepanthes sotoana* can be distinguished from *L. montis-narae* by the oblong petals (*vs.* ovate), the lateral lobes of the lip touching apically each other and do not hide the column, which is placed just above the lip (lateral lobes of the lip hide the column and do not touch each other apically) and the appendix of the lip is conic (*vs.* oblong) and conspicuous, up to 1 mm long (*vs.* inconspicuous, less than 1 mm long). We have not seen specimens of *Lepanthes schizocardia* in Costa Rica.

ACKNOWLEDGEMENTS. We acknowledge the scientific services of Ministerio del Ambiente, Energía y Telecomunicaciones de Costa Rica (MINAET) and Sistema Nacional de Áreas de Conservación (SINAC) for issuing the Scientific Passports under which wild specimens treated in this study were collected. The present paper is part of the Project 814-A7-015, “Inventario y taxonomía de la flora epífita de la región Neotropical — Orchidaceae”, sponsored by the Vice-Presidency of Research, University of Costa Rica.

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STANHOPEINAE MESOAMERICANAE, V. EL AROMA FLORAL DE LAS STANHOPEAS DE MEXICO

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ABSTRACT. Analyses of the floral fragrances of 12 of the 13 species of *Stanhopea* from México are presented here. Some of the species, such as *S. hernandezii*, *S. martiana*, *S. tigrina*, *S. intermedia* and *S. graveolens* are well characterized by their floral fragrances, while the other two species *S. ruckeri* and *S. intermedia* have two chemotypes. Furthermore, there exist two groups of 3 species each which are not delimited by their floral fragrances, just as their taxonomy and morphology also are not easily described and clear. .

RESUMEN. Se presentan análisis de aromas florales de 12 de las 13 especies de *Stanhopea* de México. Algunas, como *S. hernandezii*, *S. martiana*, *S. tigrina*, *S. intermedia* y *S. graveolens*, se pueden caracterizar muy fácilmente por su olor, mientras que otras dos especies, *S. ruckeri* y *S. intermedia*, presentan dos quimotipos. Además, existen dos grupos con tres especies cada uno que no se delimitan por sus aromas; igual, su taxonomía y morfología no es fácil y clara.

PALABRAS CLAVE / KEY WORDS : Orchids, Orquídeas, *Stanhopea*, México, floral fragrances, aromas florales

Este artículo está dedicado a Miguel Ángel Soto Arenas quien falleció víctima de un asesinato. Miguel era un gran amante de las *Stanhopea* y por esta razón contribuyó bastante al conocimiento de este género. Él no solamente es autor de dos especies de *Stanhopea* de Mexico (*Stanhopea dodsoniana* Salazar & Soto Arenas, *Stanhopea whittenii* Soto Arenas, Salazar & G.Gerlach), sino también, ha visto y colectado la gran mayoría de ellas en su habitat natural. Sin él mi parte para la *Flora Mesoamericana* hubiera sido muy pobre, porque él puso a mi disposición los datos básicos de las especies de *Stanhopea* de México. Pensé en publicar este trabajo con los aromas florales de las *Stanhopea* de México al terminar de investigar todas las especies, pero la muerte de Miguel me impidió de hacerlo; ahora sin incluir la *S. maculosa*, la cual todavía no ha florecido en el Jardín Botánico de Munich, he decidido publicar el trabajo prematuramente.

Introducción

El género *Stanhopea* está presente en México con 13 especies aquí reconocidas (Tab. 1). Todos pertenecen al subgénero *Stanhopea* y aquí a las secciones *Saccata* y *Wardii*. México representa un segundo centro de

diversidad del género; el otro es en Colombia con 19 especies de los 3 subgéneros y en las 4 secciones. Con *Stanhopea maculosa*, la subtribu Stanhopeinae encuentra su límite norte de distribución en el Edo. de Sonora, en los bosques de encinos y pinos en un habitat con un período de sequía muy pronunciado. Todo el resto de las especies de *Stanhopea* de México se encuentra meridional del Trópico de Cáncer, en climas calientes o templados, en bosques y selvas húmedas.

Las especies de *Stanhopea* de México según Gerlach (1999) se agrupan en:

Sección *Saccata*¹

S. hernandezii [= *S. cavendishii* Lindl. ex W.Baxter, *S. devoniensis* Lindl., *S. expansa* P.N.Don, *S. lyncea* (Lindl.) P.N.Don]

S. intermedia Klinge (= *S. novogaliciana* S.Rosillo)
S. maculosa Knowles & Westc. (= *S. fregeana* Rchb.f.,
S. marshii Rchb.f., *S. schilleriana* Rchb.f.)

S. martiana Lindl. (= *S. implicata* Westc. ex Lindl., *S. velata* C.Morren)

S. pseudoradiosa Jenny

¹ La lista de sinónimos no está completa. Se mencionan solamente los más conocidos y usados.

TABLA 1. Lista de plantas investigadas.

Especie	Numero	Origen	Elevación
<i>S. dodsoniana</i>	99/3327	Edo. Chiapas, weniger als 10km vor Ocosingo aus Richtung San Cristobal	
<i>S. graveolens</i>	02/2290	Edo. Chiapas, Lagunas de Monte Bello	
<i>S. hermandezii</i>	92/3098	Edo. México, Toluca	
<i>S. intermedia</i>	99/3313	Guerrero, Atoyac de Alvarez, 6 millas de El Pareiso hacia Atoyac; sobre el camino Atoyac-Xochipala	1100 m
<i>S. intermedia</i>	Soto 3131	sin	
<i>S. intermedia</i>	00/3843	sin (<i>S. novogaliciana</i>)	
<i>S. martiana</i>	99/3315	Edo. Oaxaca, Km 170 de la carretera Oaxaca-Pto. Escondido	1840 m
<i>S. martiana</i>	99/3317	Edo. Jalisco (sin datos precisos)	
<i>S. oculata</i>	73/577	Guatemala (sin datos precisos)	
<i>S. pseudoradiosa</i>	99/3316	Edo. Oaxaca, Dto. Juquila, km 12.2 de la brecha de Luz de Luna a Miahuatlán; que conecta las carreteras 131 y 175	1250 m
<i>S. pseudoradiosa</i>	08/0915	sin	
<i>S. ruckeri</i>	Soto 5115	sin	
<i>S. ruckeri</i>	99/3300	Edo. Chiapas, Ocosingo, Crucero Corozal, 144 km al SE de Palenque; por la carretera a Marqués de Comillas	150 m
<i>S. radiosa</i>	99/3302	Edo. Nayarit (sin localidad precisa)	
<i>S. radiosa</i>	99/3319	Edo. Sinaloa, km 223 carretera Durango-Mazatlán, cerca de Potrerillos	1350 – 1400 m
<i>S. radiosa</i>	99/3339	sin	
<i>S. saccata</i>	99/3323	Edo. Chiapas, km 30 del carretera Huixtla-Motozintla	1000 m
<i>S. tigrina</i>	98/2068	Edo. Tamaulipas, Gómez Farias	
<i>S. tigrina</i>	07/09/90	sin	
<i>S. tigrina</i>	10/16/96	sin	
<i>S. whittenii</i>	99/3306	Edo. Chiapas, Municipio: Comitán de Domínguez, km 11; camino al ejido de Las Margaritas	1500 m

S. radiosa Lem.

S. saccata Batem.

S. tigrina Batem. ex Lindl. [= *S. nigroviolacea* (C.Morren) Beer]

Sección *Wardii*

S. dodsoniana Salazar & Soto Arenas

S. graveolens Lindl. (= *S. aurata* Beer, *S. venusta* Lindl.)

S. oculata (= *S. minor* Schltr., *S. purpusii* Schltr.)

S. ruckeri Lindl. (= *S. inodora* Lodd. ex Lindl.)

S. whittenii Soto Arenas, Salazar & G.Gerlach

Materiales y Métodos

Muestras de las plantas investigadas están depositadas en el Herbario del Botanische Staatssammlung München (M). Las flores están conservadas en líquido en una solución de agua /

alcohol etílico / formol / ácido acético / glicerina (40/45/5/5/5).

Para la colecta del aroma floral, la planta era observada en la mañana del primer día de su floración. La inflorescencia era puesta en un recipiente de vidrio de un tamaño adecuado. El recipiente se tapaba con una hoja de aluminio. El aire cargado del perfume floral se succionaba con una bomba pequeña (personal air sampler) atravesado por un filtro de carbotrap por 3 a 4 horas (headspace technique). Después las sustancias absorbidas por el filtro fueron diluidas en hexano de alto grado de pureza e inyectadas en un cromatógrafo de gases. La identificación de ellas fue hecha con un espectrómetro de masas y con su tiempo de retención en una columna polar (WAX fase). Todos los análisis eran realizados por R. Kaiser en el laboratorio de Givaudan en Dübendorf, Suiza (Fig. 1—2).

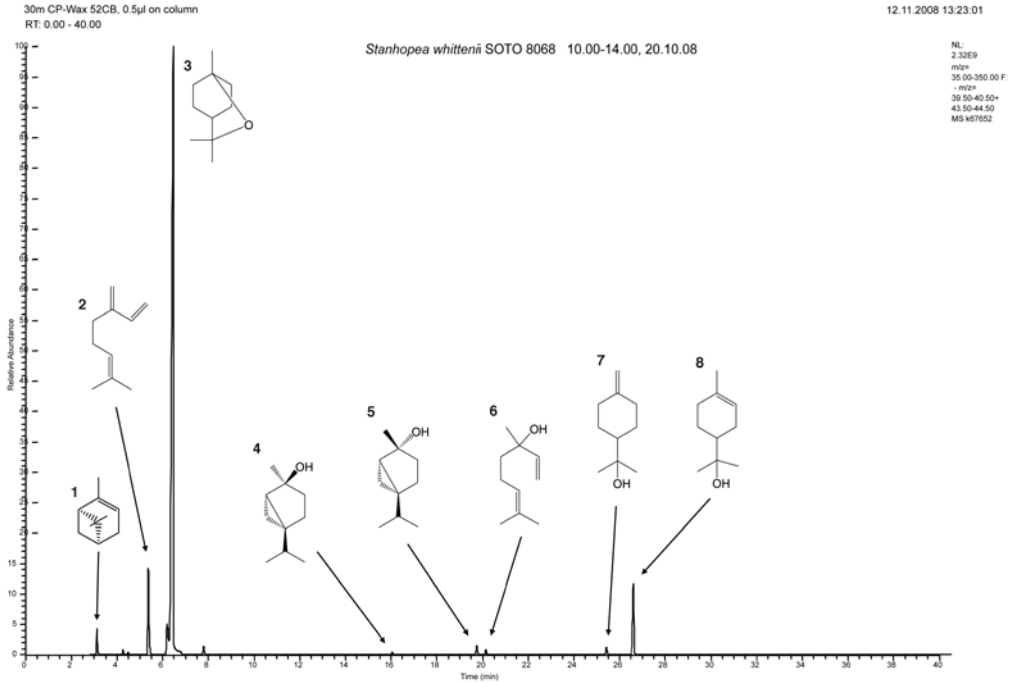


FIGURA 1. Chromatograma del aroma floral de *S. whittenii* SOTO 8068. 1 - β -Pinene, 2 - Myrcene, 3 - Eucalyptol, 4 - trans-Sabinene hydrate, 5 - cis-Sabinene hydrate 6 - Linalool, 7 - δ -Terpineol, 8 - α -Terpineol (generosidad de R. Kaiser).

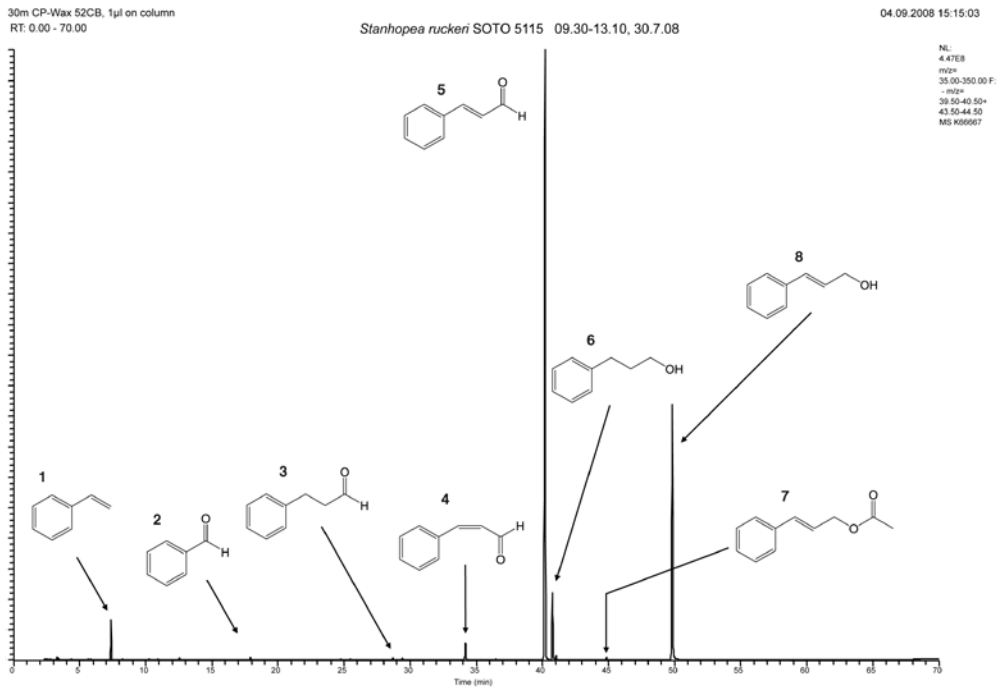


FIGURA 2. Chromatograma del aroma floral de *S. ruckeri* SOTO 5115. 1 - Styrene, 2 - Benzaldehyde, 3 - 3-Phenylpropanal, 4 - (Z)-Cinnamic aldehyde, 5 - Cinnamic aldehyde, 6 - 3-Phenylpropanol, 7 - (E)-Cinnamyl acetate, 8 - (E)-Cinnamic alcohol (generosidad de R. Kaiser).

	<i>S. radiosa</i> 99/3302	<i>S. radiosa</i> 99/3339	<i>S. radiosa</i> 99/3319	<i>S. radiosa</i> 99/3316	<i>S. pseudoradiosa</i> 08/0915	<i>S. pseudoradiosa</i> 08/0915	<i>S. saccata</i> 99/3323	<i>S. herrandezii</i> 92/3098	<i>S. martiana</i> 99/3315	<i>S. martiana</i> 99/3317	<i>S. tigrina</i> 09/07/90	<i>S. tigrina</i> 10/16/96
α-Pinene	1.2	1.2	4	2.7	1	1.2	0.6	0.4	0.1	0.1		
Butyl Acetate	0.03				0.6							
Hexanal					0.6							
β-Pinene	0.3	0.2	0.6		0.2	0.2		0.01		0.01		
Sabinene	0.2	0.1	0.2	0.4	0.2				0.01			
Myrcene	1.5	1.2	2	1.5	0.6	0.8	0.2	0.1	0.1	0.1		
Limonene	1.4	0.1	0.5	1.1	6.2	0.8	0.1	0.1	0.03	0.04	0.02	0.02
Eucalyptol	25.5	68.8	57	23.5	3.1	15.9	0.2	2.3	1	1.7	0.1	0.2
(Z)-Ocimene	0.2	0.05	0.07	0.4	0.4	0.4	0.5					
(E)-Ocimene	17.8	2.2	13	40	74.6	30	87.3					
Styrene												
Hexyl acetate								0.1	0.01	0.03		
Terpinolene												
Hexanol					0.3					0.01		
(Z)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene	0.6	1.7	0.8	1.6	0.1	1.1						
Acetoine		0.4	0.2									
Nonanal	0.02				0.05		0.08		0.01	0.01	0.03	
(E)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene	0.9	2.3	1.3	3.5	0.2	2	0.7					
6,7-Epoxy-myrcene (Myrcene epoxide)	0.03	0.1	0.1									
p-Methylanisole				0.03		0.02						
Rosefuran	0.05			0.3								
(Z)-Ocimene epoxide	0.1	0.2		0.4		0.2	0.1					
trans-Sabinene hydrate		0.1										
Acetic acid			2				0.08				0.08	
(E)-Ocimene epoxide	0.9	1.4	1.3	4	0.3	3.1	1.3					
Decanal	0.01				0.05		0.06					
Benzaldehyde	1.8	1	2.8	0.6		0.2	0.05	0.4	0.02	0.02	0.2	0.02
cis-Sabinene hydrate	0.1	0.3	0.2									
Linalool	0.2	0.5	0.2	0.2	0.2	0.2	0.1	0.1	29.7	7	0.05	0.02
Octanol	0.01						0.2					
Terpinen-4-ol												
Methyl benzoate	2.9	0.6	1	0.9	0.1	0.1		0.5	0.4	0.2	0.9	0.03
cis-β-Terpineol												
δ-Terpineol	0.4		0.1									
α-Terpineol	0.9	1.6	1.1			0.2			0.01	0.01		0.05
Benzyl acetate								11.6	0.02	0.04	1.4	3.2
(E,E)-α-Farnesene								13	0.5	0.2		
1,4-Dimethoxybenzene	0.02	0.1				0.6						
Methyl salicylate	0.07	0.1	0.1	0.2				0.6	1.1	3	1.6	0.2
Phenylethyl acetate									63.3	86	93.5	90.1
(E,E)-2,6-Dimethyl-3,5,7-octatrien-2-ol	0.2				0.05		0.6					
Methyl 3-phenylpropionate	0.9					0.2						
Benzyl alcohol	0.3	0.2	0.6	0.1				0.2	0.01	0.01	0.1	0.1
(Z)-Cinnamic aldehyde		0.4	0.2			0.1						
Phenylethyl alcohol				1.1					0.3	0.4	0.7	0.8
Phenylacetone nitrile								3				
3-Phenylpropyl acetate	0.07	0.07	0.05									0.05
Methyl (Z)-cinnamate	0.06					0.6						
Cinnamic aldehyde	9.3	5.4	6.2	0.03	0.08	1.5	0.07					
3-Phenylpropanol	1.8	1.2	2									
(E)-Nerolidol												
Methyl (E)-cinnamate	26.4				0.3	35						
(E)-Cinnamyl acetate								64				
Methyl anthranilate								0.02	0.05			0.02
(E)-Cinnamic alcohol	0.06						0.1	0.1				4.2
p-Methoxyphenylethyl acetate												0.04
Indole								3	3.3			0.6
Vanilline									0.02	0.04	0.2	
Benzyl benzoate								0.2			0.2	

continúa

TABLA 2. Análisis de aromas florales.

	<i>S. tigrina</i> 99/2068	<i>S. novogaliciana</i> 00/3843	<i>S. 99/3313</i>	<i>S. intermedia</i> Soto 3131	<i>S. dodsoniana</i> 02/2291	<i>S. dodsoniana</i> 99/3327	<i>S. oculata</i> 73/577	<i>S. whiteni</i> 99/3306	<i>S. whiteni</i> Soto 8068	<i>S. ruckeri</i> 99/3300	<i>S. ruckeri</i> Soto 5115	<i>S. graveolens</i> 02/2290
α -Pinene	0.1	1.4	2	1.7	0.9	3.8		2.1	1.5	0.3		2.8
Butyl Acetate												
Hexanal										0.05		
β -Pinene	0.02	0.4	0.4	0.4	0.3	1	0.3	0.4	0.3			0.7
Sabinene		0.2	0.3	0.4	0.2	0.6	0.2	0.3	0.2	0.1		0.5
Myrcene	0.04	9.2	6.8	6	6.8	6.7	3.6	7.5	7	0.04		11.4
Limonene		2	2.7	3.5	4.3	3	0.5	4	3.6	0.5	0.04	7
Eucalyptol	0.8	75	48.5	65.5	67.5	75	68	81.8	76.9	0.1		49
(Z)-Ocimene		0.02		0.01	0.02	0.01	0.1		0.01			
(E)-Ocimene	0.01	0.7	0.5	0.3	0.7	0.4	0.4	0.4	0.7			
Styrene										0.07	2.8	
Hexyl acetate	0.04											
Terpinolene		0.06	0.04	0.02	0.03	0.04	0.05					
Hexanol				0.04						0.1	0.1	
(Z)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene												
Acetoino											0.04	
Nonanal		0.02			0.01	0.01		0.03		0.07	0.2	
(E)-3(4)-Epoxy-3,7-dimethyl-1,6-octadiene												
6,7-Epoxy-myrcene (Myrcene epoxide)		0.04		0.02	0.02	0.02		0.05	0.02			0.05
p-Methylanisole				0.01						0.03		
Rosefuran												
(Z)-Ocimene epoxide												
trans-Sabinene hydrate		0.2	0.2	0.1	0.2	0.2	0.2	0.2	0.2			0.7
Acetic acid												
(E)-Ocimene epoxide												
Decanal						0.01						0.04
Benzaldehyde	0.01	0.2	0.2	0.2						0.2	0.2	
cis-Sabinene hydrate		0.6	0.5	0.2	0.9	0.6	0.2	0.2	0.8			1.8
Linalool	0.04	0.2	0.4	0.2	0.5	0.3	0.4	0.04	0.5	0.03		1.3
Octanol										0.03	0.04	
Terpinen-4-ol			0.03	0.01	0.02	0.01	0.2	0.03	0.03	0.04		0.1
Methyl benzoate		0.3	0.9	0.03								
cis- β -Terpineol		0.04	0.04	0.02	0.08	0.05	0.4	0.03	0.05			0.1
δ -Terpineol		0.5	0.7	0.3	1.2	0.6	1	0.08	0.7			1.3
α -Terpineol	0.07	7	5.3	2.4	15.1	6.8	13.7	1.1	7.1			10.6
Benzyl acetate	2		0.4	0.1		0.05						
(E,E)- α -Farnesene			12	7.8							0.2	1.1
1,4-Dimethoxybenzene												
Methyl salicylate	0.2											
Phenylethyl acetate	87		2.3	3.1		0.01		1.5		2.7	0.01	0.2
(E,E)-2,6-Dimethyl-3,5,7-octatrien-2-ol												
Methyl 3-phenylpropionate												
Benzyl alcohol		0.1	0.3	0.2				0.01		0.1	0.01	
(Z)-Cinnamic aldehyde											1.6	
Phenylethyl alcohol	1.5		0.2	0.5				0.01		90.3		
Phenylacetone nitrile												
3-Phenylpropyl acetate											0.07	
Methyl (Z)-cinnamate												
Cinnamic aldehyde											61	
3-Phenylpropanol											6.4	
(E)-Nerolidol			0.01	0.01						0.08	0.5	0.03
Methyl (E)-cinnamate												
(E)-Cinnamyl acetate	6.4			0.01							0.2	
Methyl anthranilate			0.1	0.1				0.01				
(E)-Cinnamic alcohol	0.06										25	
p-Methoxyphenylethyl acetate	0.05		0.4	0.07								
Indole	1.4		13	6.3	0.6		9.2					10
Vanilline					0.2	0.03	0.2					
Benzyl benzoate							0.2		0.01			

TABLA 2. Análisis de aromas florales.

Resultados y Discusión

No todas las sustancias presentadas en la Tabla 2 tienen importancia en la atracción de los polinizadores, pero en la mayoría de los casos no sabemos si son percibibles por estos animales o no. Hay muchas sustancias que son comunitarias como mencionan también Whitten & Williams (1992), entre estas especialmente los monoterpenos (α -pineno, β -pineno, sabineno, mirceno, limoneno, eucaliptol (1,8-cineol) y los ocimenes). Sabemos que entre ellos hay unos de los más fuertes atrayentes para los euglosidos, pero como están presentes en casi todas las especies no pueden servir como rasgos diferenciales. Como consecuencia estas sustancias no están consideradas en la discusión.

SECCIÓN SACCATA

a) Grupo de *S. saccata* (*S. pseudoradiosa*, *S. radiosa* y *S. saccata*)

Estas tres especies forman un grupo de gran similitud morfológica. Tienen el labelo profundamente saccato y una coloración muy parecida de amarillo hasta crema con una puntuación muy fina, pero nunca con manchas. Se diferencian especialmente en el tamaño y la forma de la apertura del hipoquilo. Jenny (2004) muestra muy bien un gradiente de aperturas en 5 especímenes de *S. radiosa* y *S. pseudoradiosa* en sus figuras 267 y 268 (p.178)². Poniendo estos labels con este de *S. saccata* (Fig. 5F) en línea uno puede observar un gradiente de anchura de las aperturas de *S. pseudoradiosa* (Fig. 3D) a *S. radiosa* (Fig. 5D) hacia *S. saccata*. Las tres especies provienen del lado pacífico de la Sierra Madre Occidental pasando por la Sierra Madre del Sur a Chiapas llegando hasta Honduras. La más norteña es *S. radiosa*, la sureña *S. saccata*. Entonces el gradiente de la apertura no se refleja en la distribución. Según Jenny las especies no crecen mixtas, pero todavía hay muy pocas observaciones para comprobar éste factor con seguridad.

Las 8 muestras de aroma publicadas por Whitten & Williams (1992) y las 7 muestras adicionales presentadas aquí tienen (E)-ocimeno como componente significante en porcentajes entre 2,2% y

² La foto esta invertida, o hay que cambiar izquierdo por derecho.

87,3%. El cinamato de metilo junto con sus derivados representa otra característica en algunos clones. En la Tabla 2 se presentan dos análisis de la misma planta de *S. pseudoradiosa* realizados en dos floraciones diferentes; es interesante ver la variabilidad del aroma floral. Quiero sumarme a la opinión de Whitten & Williams que en este grupo empieza una especiación alopatrica.

b) *Stanhopea intermedia* y *S. novogaliciana*

Por su morfología floral las dos especies no se pueden distinguir. Conservadas en líquido y así descoloridas flores de las dos especies no se pueden diferenciar. Únicamente el color es el carácter diagnóstico para las dos, *S. intermedia* es casi unicolor de un amarillo pálido (Fig. 4A, 5A), mientras *S. novogaliciana* tiene el color amarilla fuerte con manchas grandes marrones en las bases de los pétalos y del labelo (Fig. 5C). Rosillo (1984) publica otro argumento para la diferencia de las dos. Él dijo que las dos crecían juntas en la misma barranca, pero solamente la *S. novogaliciana* era visitada por euglosidos de color azul metálico, mientras que la *S. intermedia*, igual en flor no atraía ninguna abeja. Es frecuente si uno ve varias Stanhopeinae de la misma especie en un sitio en flor que unos estén visitados fuertemente mientras que otros carecen de visitantes. Eso depende del comportamiento de los euglosidos, cuales andan frecuentemente en pequeños grupos. Aparecen en una inflorescencia, pelean entre ellos por los aromas y después de cierto tiempo se van. Por esta razón supongo que era un efecto casual. Observaciones al respecto serían muy agradecidas!

La composición del aroma floral de las dos se diferencia bien. Las sustancias mayoritarias comunes de las dos son: mirceno, limoneno, eucaliptol y α -terpineol. La *S. novogaliciana* investigada contiene mucho menos componentes en el aroma floral, le faltan el indol y el (E,E)- α -farneseno como componentes de alta concentración. Puede ser que se trata de un artefacto en la recolección del aroma, porque el indol no es muy volátil y por esta razón se colecta con más dificultad y especialmente a temperaturas bajas. Por otro lado también se puede aclarar con la presencia de dos quimotipos que tenemos también en otras especies, por ejemplo en *S. ruckeri*, una especie con un concepto morfológico bien claro.

La declaración de Rosillo (1984) del euglosido azul comparándole con el polinizador de *S. radiosa* (por el tamaño), nos guía a una especie del género *Euglossa*; con alta probabilidad se trata de *Euglossa mixta* una especie con amplia distribución. Por la morfología tan similar de ambos y el crecimiento en la misma región se hace bien visible que se trata de una sola especie que aparece en dos coloraciones diferentes y dos quimotipos. Por las reglas del código botánico hay que usar el nombre mas antiguo, así *S. novogaliciana* cae en la sinonimia de *S. intermedia*.

c) Resto de la Sección (*S. hernandezii*, *S. maculosa*, *S. martiana* y *S. tigrina*)

En la taxonomía del resto de la sección no hay problemas en la delimitación de las especies. Todas tienen el epiquilo con los márgenes erectos, formando un V en corte transversal, así con el ápice tridentado, con la punta central en la mayoría de las especies mas cortas que los laterales. Todos tienen manchas, a veces muy grandes y en algunos clones de *S. tigrina* ocupando todo el superficie, dejando solamente los márgenes en su color basico (*S. tigrina* f. *nigroviolacea*).

Estas especies son endémicas de México, vienen de bosques mesophyticos desde los Edos. de Sonora y Tamaulipas en el norte hasta Oaxaca y Veracruz en el sur.

La composición química de la fragancia de tres especies de este grupo fue analizado, dejando solamente *S. maculosa* sin investigación de aroma floral. El aroma floral de *S. martiana* (Fig. 4B) y *S. tigrina* (Fig. 6A) está dominado por el acetato de feniletilo, una sustancia de aroma muy fuerte y pesado. Las dos se diferencian en su aroma por tener acetato de benzilo y salicilato de metilo en *S. tigrina* y linalool en *S. martiana* en porcentajes mayores. *S. hernandezii* (Fig. 3B) tiene un aroma bien diferente de las dos, reminiscente a canela. Grandes cantidades de acetato de cinamilo y acetato de benzilo son responsable de este olor. Estas tres especies se caracterizan muy bien por su aroma floral, no haya problema de indentificarlas con este caracter.

SECCIÓN WARDII

a) Grupo de *S. oculata* (*S. dodsoniana*, *S. oculata* y *S. whittenii*)

Este grupo es el más difícil en su taxonomía entre

todas las especies de *Stanhopea*. Las plantas vienen desde la Sierra Madre Oriental hasta Nicaragua. *S. oculata* (Fig. 3C) es conocida de los Edos. de San Luis Potosi, Puebla, Veracruz, Oaxaca y Chiapas de México llegando hasta Nicaragua en el sureste, *S. dodsoniana* (Fig. 5B) de Veracruz, Oaxaca y Chiapas y llega también a Nicaragua, mientras que *S. whittenii* (Fig. 6B) tiene su distribución desde Chiapas en México hasta Guatemala y Belice. Entonces en el Edo. de Chiapas todas las tres están presentes, *S. dodsoniana* y *S. oculata* tienen la distribución en los Edos. de Veracruz, Oaxaca y Chiapas en común. Según el aroma floral las tres se diferencian por detalles insignificantes: aunque hay unas 30 muestras de aroma investigadas, todavía no se ha detectado un carácter discriminador. Es probable que hay híbridos naturales en las muestras investigadas, porque son morfológicamente bien parecidos y hay algunos clones que son intermedias en su forma entre dos especies. Aunque estas tres especies son las mas comunes de las Stanhopeas de México todavía casi no hay datos de su polinización. Según Whitten & Williams (1992) Dodson & Williams observaron la polinización por *Eufriesea caeruleascens* en Chiapas de una planta traída de un jardín de Oaxaca. Como en esta época solamente se conocía *S. oculata*, no podemos decir con seguridad si trataba verdaderamente de esta especie. Aquí unicamente la observación de la polinización y el estudio de poblaciones puede aclarar la confusión al respecto de su taxonomía.

b) *S. ruckeri*

Los dos clones investigados de *S. ruckeri* presentan un aroma totalmente diferente. Una huela muy agradable a canela (derivados de alcohol cinámico), la otra (Fig. 3E) está dominada por el alcohol y el acetato de feniletilo, así tiene un aroma pesado. Sería sumamente interesante investigar más clones de esta especie para ver si tiene dos quimotipos o si el aroma floral es muy variable.

c) *S. graveolens*

Esta especie (Fig. 3A) es la más fácil de distinguir de todas las *Stanhopea*. Su aroma es algo desagradable causado por un alto porcentaje de indol (10%). Dos clones mas de ésta especie de Guatemala fueron investigados y muestran el mismo patrón en la composición del aroma floral. Concentraciones

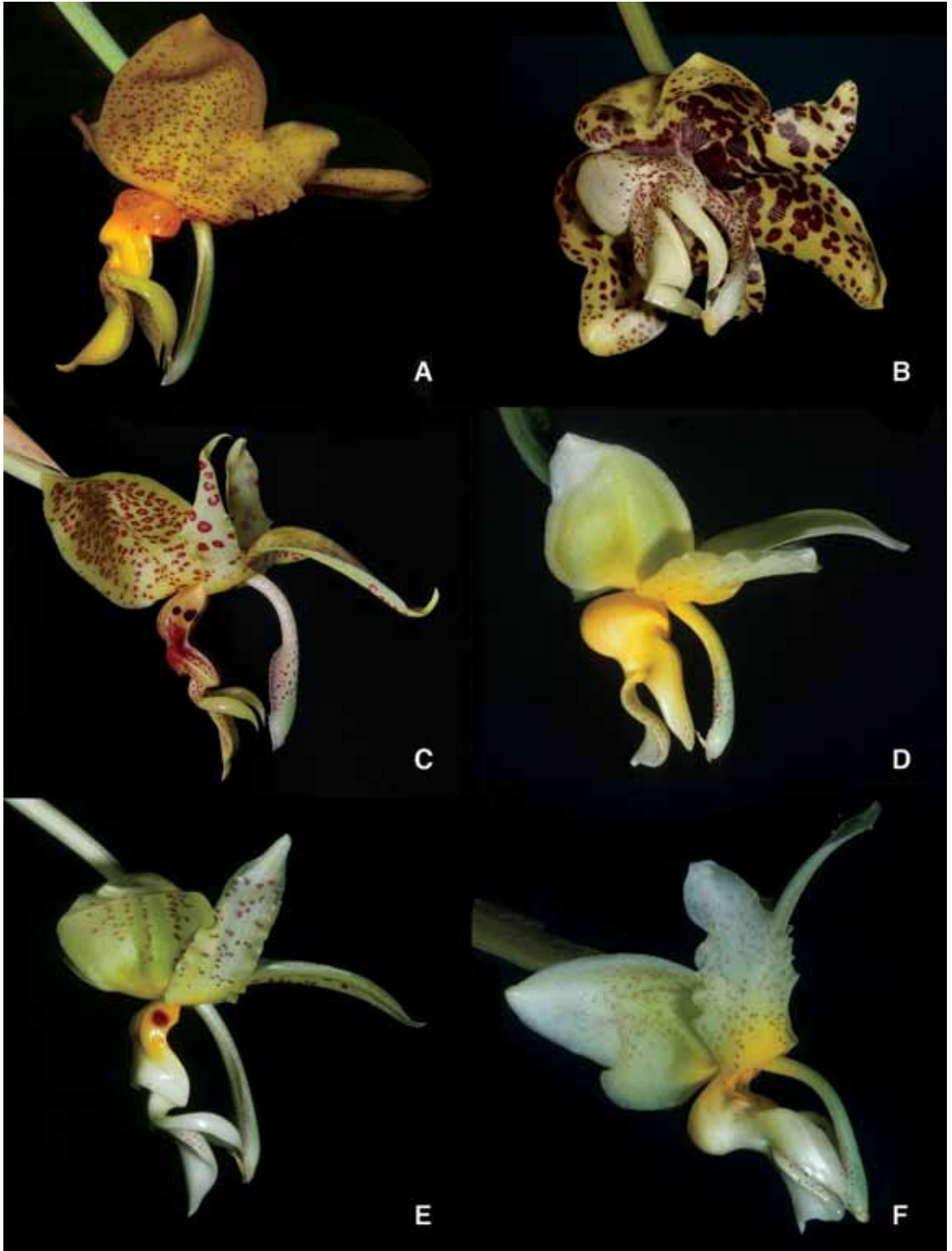


FIGURE 3. A — *Stanhopea graveolens* 02/2290. B — *S. hernandezii* 92/3098. C — *S. oculata* 73/577. D — *S. pseudoradiosa* 99/3316. E — *S. ruckeri* 99/3300. F — *S. saccata* 99/3323. Photo by G. Gerlach.



FIGURE 4. A — *Stanhopea intermedia* 99/3313. B — *S. martiana*. Photo by G. Gerlach.

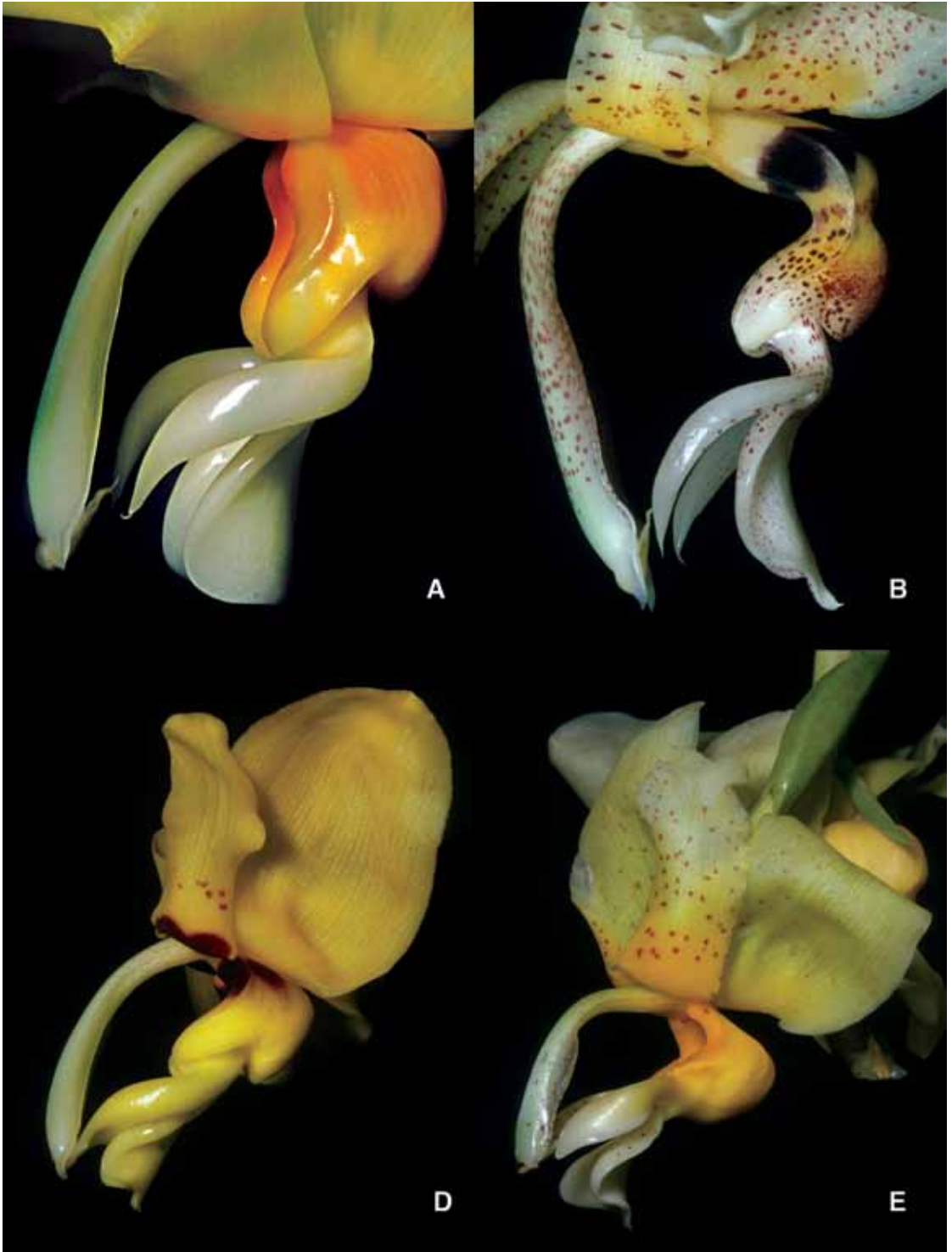


FIGURE 5. A — *Stanhopea intermedia* 99/3313. B — *S. dodsoniana* 99/3327. C — *S. novogaliciana* 00/3843. D — *S. radiosa* 99/3302. Photo by G. Gerlach.



FIGURE 6. A — *Stanhopea tigrina* 99/2068. B — *S. whittenii* 99/3306. Photo by G. Gerlach.

similares de indol se encuentran además en *S. hernandezii*, *S. intermedia* y *S. martiana*. El aroma de *S. graveolens* casi no se puede distinguir del de *S. intermedia*.

Conclusiones

Tomando en cuenta que los polinizadores de las especies de *Stanhopea* son solamente Euglósidos en la búsqueda de aromas preferidos hay que echar el ojo especialmente a este carácter. Los análisis de las aromas florales muestran que algunas especies están caracterizadas por el aroma como *S. hernandezii*, *S. martiana*, *S. tigrina*, *S. intermedia* y *S. graveolens*, mientras que otras presentan dos quimotipos o son bastante variable en su composición.

Lamentablemente las investigaciones de aromas florales están restringidas a un laboratorio y la colección del aroma floral en el campo es bastante difícil. La taxonomía está basada en muestras de herbario y descripciones que no incluyen informaciones de la fragancia de la respectiva especie. La dificultad es que son dos disciplinas que no cuadran, en el campo y en el herbario no se puede analizar los aromas, solamente al revés funciona, a tener la planta en flor uno puede hacer el análisis del aroma floral y cuadrarlo con el polinizador y la taxonomía. Este método consume mucho tiempo, así hay pocos colegas que investigan en esta dirección. Observar plantas en el campo en muchas ocasiones es un caso de suerte, primero la floración es muy corta (2 a 4 días), segundo la ó las plantas observadas deben de estar al alcance del observador y no en el dosel; además, el tiempo debe ser suficiente para que lleguen los polinizadores. Como es impredecible saber si uno puede tener éxito en estas observaciones, es más probable que este trabajo pueda ser llevado a cabo por un aficionado o científico que no depende de la carrera. Es imposible proponer a estudiantes un tema como tal para una tesis, por sus resultados impredecibles. De todos modos quiero animar a todos los amantes de

la naturaleza para que vayan al campo: necesitamos urgentemente informaciones de este tipo.

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***CROSSOGLOSSA SOTOANA* (ORCHIDACEAE: MALAXIDEAE),
A NEW SPECIES HONORING THE LATE MEXICAN BOTANIST,
MIGUEL ÁNGEL SOTO ARENAS**

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ABSTRACT: *Crossoglossa sotoana*, a new species from Costa Rica, is described and illustrated. It is compared with Ecuadorian *C. barfodii*, from which it differs by the strongly undulate margins of the leaves, the resupinate flowers, the shorter and congested inflorescence, the porrect, incurved petals, the obovate-subpandrate lip and the callus composed by two transversely rectangular lamellae. It can be distinguished from *C. boylei*, also from Ecuador, by its shorter inflorescence, the ligulate petals and the shortly caulescent plants.

KEY WORDS: Orchidaceae, Malaxideae, *Crossoglossa*, *C. sotoana*, Costa Rica, new species

Robert L. Dressler and Calaway H. Dodson created *Crossoglossa* in 1993 to accommodate several species previously placed in *Microstylis* (Nutt.) Eaton section *Blephariglottis* Schltr., together with some misfit species of *Liparis* Rich. and *Malaxis* Sol. ex Sw. (Dressler & Dodson, 1993). *Crossoglossa* can be distinguished from the latter genera by the lack of pseudobulbs, the more or less elongate stems with several distichously arranged leaves, the short, straight column clasped by basal lobes or auricles of the lip, the incumbent anther (shared with *Liparis*), and the structure of the fruit, with the wide valves being thin and papery and the narrow ones being thick and woody and free of connecting tissue. The genus is typified by *Crossoglossa blephariglottis* (Schltr.) Dressler. In 1999, in their studies on *Liparis*, Garay and Romero reduced *Crossoglossa* (as *Crassoglossum*) as a synonym under *Liparis* sect. *Tipuloidea* (Ridl.) Garay & G. A. Romero, a group diagnosed by non-pseudobulbous plants with ascending stems from a decumbent base, basally imbricate by the bases of distichous leaves not articulated with leaf-sheaths; and a short column reminiscent of that of *Malaxis* (Garay & Romero-González, 1999). DNA studies by Salazar (cited in Cribb, 2005) seem to confirm a close relationship of *Crossoglossa* with *Liparis*, with the species of the former genus forming the sister

group to a complex of Central American *Liparis*. Even though at this time there are no published phylogenetic analyses including species referable to *Crossoglossa*, Noguera-Savelli and her co-workers (2008) suggest that in future generic realignments within the Malaxideae, *Crossoglossa* could be included in a more broadly defined genus, most likely in *Liparis*. However, updated phylogenetic results currently being prepared for publication demonstrate that *Crossoglossa*'s closest relatives are the reptant Andean "*Liparis*" such as "*L. crispifolia*" and "*L. wagneri*". *Crossoglossa* is only distantly related to the clade that includes the type species of *Liparis* [*L. loeselii* (L.) Rich.] and, according to DNA sequences of ITS and matK, deserves to be maintained as distinct (G.A. Salazar, pers. comm., 2009).

As actually circumscribed, *Crossoglossa* includes some 25 species, mainly distributed in southern Central America and Andean South America, from Colombia to Bolivia, with the highest diversity found in Colombia and Ecuador. No species have been recorded from Venezuela so far (Noguera-Savelli *et al.*, 2008). The number of taxa rapidly diminishes toward the north, with a single species recorded in Nicaragua (Hamer, 2001). The real diversity of the genus, however, is still unclear, considering that more than half of the species attributed to *Crossoglossa*

were published in the last 15 years, after the proposal of the genus (Dressler & Dodson, 1993; Dodson, 1995; Ortíz, 1995; Dressler 1997; Vásquez, 1999; Pupulin, 2000; Szlachetko & Margonska, 2001; Noguera-Savelli *et al.*, 2008). Here we describe a new species from Costa Rica:

Crossoglossa sotoana Pupulin & Karremans, *sp. nov.*

TYPE: COSTA RICA. Alajuela: San Ramón, Ángeles, Alberto M. Brenes Biological Reserve, 10°13'06" N 84°36'11" W, 800-900 m, shores of Río San Lorencito, near the Terciopelo Trail, 22 May 2004, flowered in cultivation at Lankester Botanical Garden, University of Costa Rica, 5 Apr. 2005, *D. Bogarín 817* (holotype, USJ; isotype, JBL).

Similis *Crossoglossae barfodii* Dodson, a qua recedit foliis marginibus valde undulatis, floribus resupinatis, inflorescentia congesta multo brevior, petalis linearibus incurvis, labello obovato-sub-pandurato callo duobus transverse rectangularibus lamellis composito.

Terrestrial, erect *herb*, to 15 cm tall excluding the inflorescence. *Roots* finely pubescent, pale yellow, ca. 2 mm in diameter. *Stem* terete, 3-5 mm in diameter, 4-5 cm long, laxly concealed by the leaf bases. *Leaves* elliptic-spathulate, obtuse, from a narrow, conduplicate base clasping the stem, the margins strongly undulate, 50-80 × 15-20 mm above the middle. *Inflorescence* an erect, successively many- (to 60) flowered raceme, hexagonal in section, with distinct longitudinal keels provided with glandular trichomes, to 15 cm long. *Floral bracts* triangular, acuminate, the margins with glandular hairs, 6.0-7.0 × 2.5 mm. *Ovary* terete-subconical, glabrous, proximally white, distally green, to 6 mm long including the pedicel. *Flowers* resupinate, spreading, slightly facing downwards, sepals and petals yellowish green, lip pale greenish yellow flushed with green toward the base, the central vein and the basal calli yellow; column green, anther yellow. *Dorsal sepal* ovate, rounded, 3-veined, concave toward the apex, 2.6 × 1.6 mm. *Lateral sepals* narrowly ovate, rounded, 3-veined, 2.5 × 1.5 mm, sometimes shortly connate at base. *Petals* ligulate, obtuse, 1-veined, slightly porrect-incurved in natural

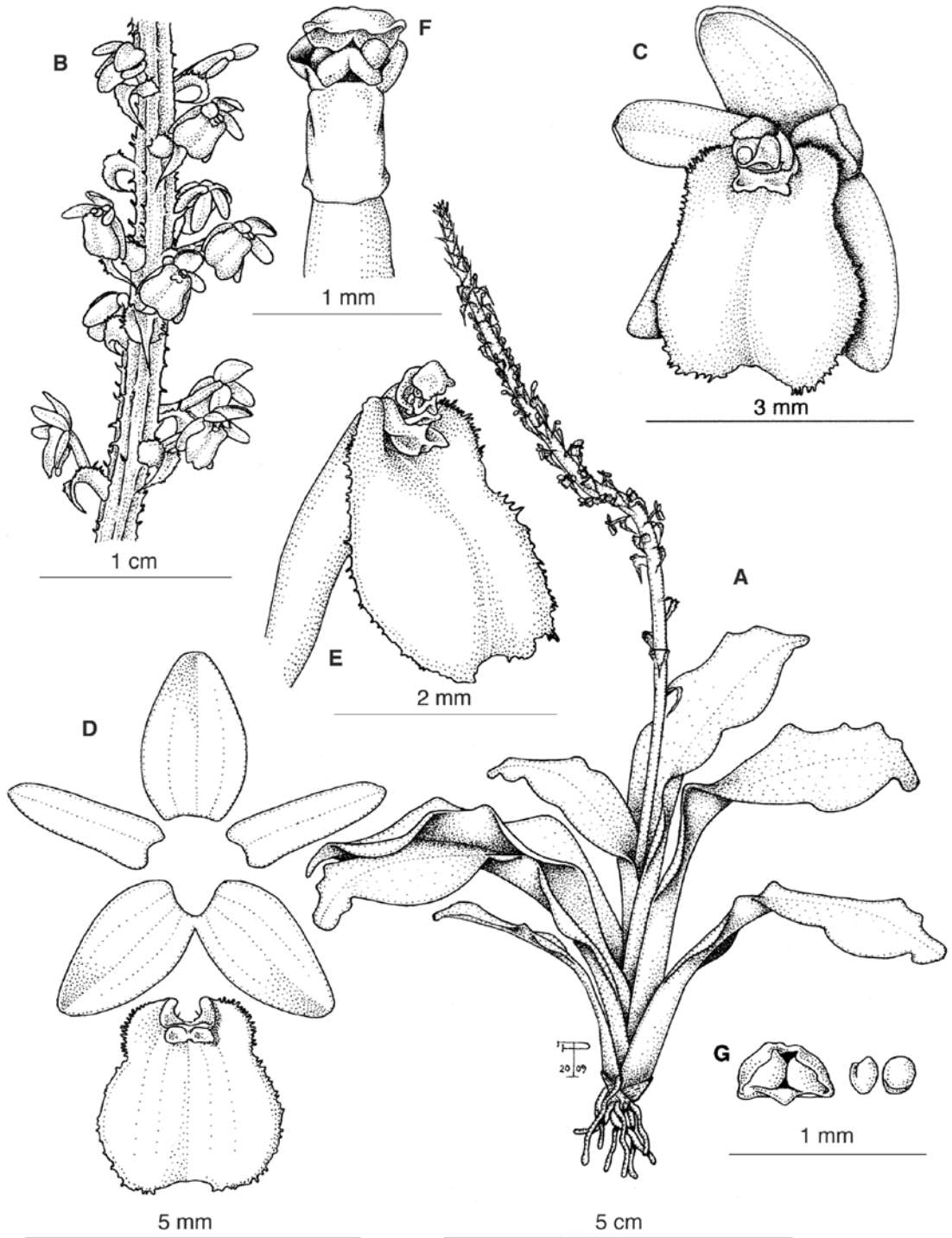
position, 2.5 × 1.0 mm. *Lip* obovate-subpandurate, retuse, 5-veined, basally concave, then convex, 3.0 × 2.8 mm, the margins finely and irregularly dentate-ciliate, the base subcordate with the auricles partially clasping the column, provided with a basal, ring-like callus around the column, the callus bearing one transversely rectangular, thickened, slightly concave projections on each side of the midvein. *Column* subterete, clavate, 1 mm long, the distal portion expanded around the subapical stigma. *Anther* cucullate, transversely elliptic-reniform, 2-celled. *Pollinia* 2, obovate-subsppherical.

DISTRIBUTION: Known only from Costa Rica.

ECOLOGY: Plants of *C. sotoana* grow as terrestrials in loose, moist soils and leaf litter in the understory of primary vegetation. The only known population of this species was found in the premontane wet forest of the Tilarán mountain range, on the Caribbean watershed of the continental divide in central Costa Rica, at about 800-900 m elevation.

EPONYMY: Named in honor of the recently deceased Mexican botanist, Miguel Ángel Soto Arenas, to commemorate his fundamental contributions to orchidology.

Crossoglossa sotoana closely resembles the Ecuadorian *C. barfodii* Dodson, but that species has flat leaves (vs. strongly undulate along margins), nonresupinate flowers (vs. resupinate), a much longer (to 30 cm vs. 15 cm), lax (vs. congested) inflorescence, subfalcate-reflexed petals (vs. linear, incurved), and an obcordiform-pandurate (vs. obovate-pandurate) lip, provided at the base with two erect, triangular lamellae (vs. low, transversely rectangular). *Crossoglossa boylei* Dodson, also from Ecuador, can be distinguished by the long caulescent plants, longer inflorescence, broadly ovate dorsal sepal and ovate petals. In Costa Rica, *C. sotoana* can be distinguished from *C. fratrum* (Schltr.) Dressler and *C. tipuloides* (Lindl.) Ktze. by the short, nearly acaulescent plants and its distinctly lobed, obovate-subpandurate, retuse lip. *Crossoglossa aurantilineata* Pupulin has longer and narrower leaves, longer floral bracts, narrower sepals and petals, and an orange stripe along the midrib of the lip, while *C. blephariglottis* (Schltr.) Dressler presents an acute lip with longer linear petals.



Crossoglossa sotoana Pupulin & Karremans. A — Habit. B — Portion of the inflorescence. C — Flower. D — Dissected perianth. E — Column and lip, oblique view. F — Column, adaxial view. G — Anther and pollinia. Drawn by F. Pupulin and J.D. Zúñiga from the holotype.

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DOS ESPECIES NUEVAS DE PLEUROTHALLIDINAE (ORCHIDACEAE) DE MÉXICO

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RESUMEN: Se describen e ilustran dos especies nuevas de la subtribu Pleurothallidinae como *Acianthera sotoana*, de Oaxaca y Veracruz, y *Stelis sotoarenasii*, de Oaxaca. Estas orquídeas habían sido confundidas previamente con especies similares, la primera con *Acianthera johnsonii*, la segunda con *Stelis retusa*. Para cada especie se proporciona información sobre distribución, hábitat, fenología, estado de conservación y un mapa de sus localidades conocidas.

ABSTRACT: Two new species of subtribe Pleurothallidinae are described and illustrated as *Acianthera sotoana*, from Oaxaca and Veracruz, and *Stelis sotoarenasii*, from Oaxaca. These orchids have been previously confused with similar species, the former with *Acianthera johnsonii*, the latter with *Stelis retusa*. For each species information about distribution, habitat, phenology, conservation status, and a map with their known localities are provided.

PALABRAS CLAVE / KEY WORDS: *Acianthera sotoana*, endemismos, Oaxaca, orquídeas, *Stelis sotoarenasii*, Veracruz

En los últimos años, la revisión de las especies de la subtribu Pleurothallidinae para México ha hecho que éste sea uno de los grupos mejor estudiados de la orquídeoflora nacional (Soto Arenas, 1987; Hágsater & Salazar, 1990; Solano Gómez 1993, 1999, 2000; Salazar & Soto Arenas, 1996; Hágsater & Soto Arenas, 2003; García-Cruz *et al.*, 2003; López-Velázquez *et al.*, 2007; Solano Gómez & Salazar, 2007; Solano Gómez *et al.*, 2008; Hágsater & Soto Arenas, 2008). La diversidad de este grupo en México está representada por 20 géneros, 203 especies y 3 taxones infraespecíficos (Soto Arenas *et al.*, 2007). Si bien para la mayoría de las especies su delimitación taxonómica ha quedado bien establecida, permanecen varias que no han sido publicadas, por lo que en este trabajo dos de ellas son publicados como nuevas a partir de material vivo y herborizado; cada especie se acompaña de un dibujo a línea detallado y se proporciona un mapa para indicar su distribución conocida en México.

Acianthera sotoana R.Solano, *sp. nov.*

TIPO: MÉXICO. Oaxaca: Municipio Totontepec Villa de

Morelos, cañón del Río Toro, sobre el banco del río, 1800 m, colectado septiembre 1977, prensado 23 julio 1983, *O. Suárez 566* (holotipo, AMO; isotipo, AMO). FIG. 1, 3.

Acianthera johnsonii (Ames) Pridgeon & M.W.Chase affinis autem laciniate-calyce pubescenti extus et intus, petalis non falcatis, labello acuto ad apicem, et habitu differt.

Hierba rupícola, a veces epífita, cortamente rizomatosa, hasta de 36.5 cm de altura. *Raíces* blanquecinas, flexuosas, de 1.2-2.0 mm de diámetro. *Rizoma* muy corto, engrosado, de 8-10 mm de longitud entre tallos adyacentes, 4.5-6.0 mm de grosor. *Tallos* erectos, cilíndricos, formados por 4-5 entrenudos, 4.0-17.5 cm de largo, 1.6-3.5 mm de diámetro; cubiertos totalmente por vainas lateralmente comprimidas, infladas hacia el ápice, imbricadas, obtusas, carinadas a lo largo de las nervaduras, caedizas, densamente manchadas de púrpura. *Hoja* sésiles, una por tallo, apical, sésil, elíptica, obtusa, coriácea, cortamente bilobada y mucronada en el ápice, ligeramente recurvada en los márgenes, 10-19 x 4-6 cm.

Inflorescencia racemosa, generalmente de la base del tallo y colgante, a veces también del ápice del tallo, erecta y reclinada sobre la superficie interna de la hoja, 5.0-6.5 cm de largo, con hasta 10 flores que abren simultáneamente, inflorescencia basal ligeramente más larga que la apical; pedúnculo cilíndrico, 1-3 cm de largo, 2 mm de diámetro, en la inflorescencia apical rodeado por una bráctea espatácea, conduplicada, triangular, obtusa, escariosa, caediza; brácteas del pedúnculo 2 en la inflorescencia apical, hasta 5 en la inflorescencia basal, oblicuamente infundibuliformes, imbricadas, obtusas, membranáceas, densamente cubiertas de manchas púrpura, 6.0-7.7 cm de largo. *Brácteas florales* similares a las del pedúnculo pero más grandes, 7.9-8.7 mm de largo. *Ovario* subpiramidal, subtriangular en sección transversal, engrosado hacia el ápice, verde con manchas púrpura, glandular-pubescente; articulado en un ángulo casi recto a un pedicelo cilíndrico. *Flores* casi perpendiculares al racimo, poco abiertas, 17-21 mm de largo; sépalos café-anaranjados o amarillo-anaranjados, densamente manchados de púrpura por ambas superficies; pétalos café-anaranjados con manchas púrpura; labelo anaranjado con manchas púrpura; columna y antera púrpura. *Sépalos* casi paralelos a la columna, carnosos, mucronados en el ápice, glandular-pubescentes en ambas superficies, los pelos rojo muy oscuro, ciliados en los márgenes; sépalo dorsal lanceolado a oblongo-lanceolado, subagudo, 7-nervado, carinado sobre la nervadura media, 17.0-18.5 x 5 mm; sépalos laterales unidos entre sí por dos tercios de su longitud para formar un sinsépalo cóncavo, carnosos, oblongo-lanceolado, bipartido, 18.4-21.5 x 10.0-13.4 mm, cada sépalo 7-nervado, carinado sobre la nervadura media. *Pétalos* paralelos a la columna, cartilagosos, lanceolado-subrómicos, oblicuos, acuminados, angulados en la mitad, ciliados en los dos tercios superiores, 3-nervados, 11.2-12.3 x 2.0 mm. *Labelo* provisto de una uña trapezoidal que se une al pie de columna, en posición natural paralelo con respecto a la columna, arqueado, carnosos, conduplicado, papiloso en la superficie interna, 3-nervado, 5.5 x 2.1 mm; cuando extendido cordado-sagitado, subagudo, 6.7 x 3.7 mm; con dos callos engrosados, subparalelos y ligeramente erectos sobre la lamina, más un callo prominente, rojizo e incurvado hacia la base. *Columna* delgada, ligeramente arqueada, el cuerpo de 5 mm de

largo y 1 mm de ancho a nivel del estigma; con un pie de columna bien desarrollado, incurvado, casi la mitad de largo que el cuerpo de la columna; clinandrio cubriendo totalmente la antera, 3-dentado. *Estigma* formado por una cavidad en la superficie ventral de la columna; rostelo ventral, laminar, convexo. *Antera* ventral, esférico-ovoide, diminutamente glandulosa en la superficie ventral, 1 mm de largo, 0.8 mm de ancho. *Polinario* formado por dos polinios ovoides, lateralmente comprimidos, amarillos, 0.6 mm de largo, unidos por caudículas granulosas.

OTROS ESPECÍMENES: MÉXICO. **Oaxaca:** Municipio Totontepec Villa de Morelos, cañón del Río Toro, sobre el banco del río, 1800 m, septiembre 1977, prensado 20 junio 1981, *O. Suárez 566* (AMO). Municipio Totontepec Villa de Morelos, cañón del Río Toro, sobre el banco del río, 1800 m, septiembre 1977, *Greenwood s.n.* (AMO). Municipio Totontepec Villa de Morelos, cañón del Río Toro, sobre el banco del río, 1800 m, septiembre 1977, *O. Suárez 2500* (OAX). Municipio Totontepec Villa de Morelos, Santa María Huitepec, río Llano, bosque de galería con *Platanus* rodeado de selva mediana perennifolia, 1497 m, 17°12'8.27"N, 96°1'28.35"O, rupícola, abundante a la orilla del río, 13 marzo 2009, *R. Solano & A. Martínez s.n.* (OAX). **Veracruz:** Municipio Pajapan, cima del volcán San Martín Pajapan, bosque mesófilo de montaña, 1125 m, 18°18'N, 94°44'O, epífita, rara, flores anaranjadas con puntos morados, 2 septiembre 2007, *T. Krömer & E. Otto 2954* (MEXU). Municipio de Tatahuicapan de Juárez, faldas del volcán Santa Martha, bosque mesófilo de montaña, 1500 m, 18°19'N, 94°50'O, epífita, rara, flores amarillas con manchas moradas, 28 agosto 2008, *T. Krömer 3696* (MEXU). Municipio Ixhuacán de los Reyes, Comapa, bosque mesófilo de montaña, 1560 m, 19°18'30"N, 97°5'10"O, rupícola, regular, con cápsulas, 19 octubre 2008, *J. Viccón & M. Castañeda 199* (MEXU).

DISTRIBUCIÓN: Esta especie es endémica de México y hasta ahora solo ha sido registrada en montañas de la vertiente del Golfo de México (Fig. 3), en el Eje Volcánico Transversal y la Sierra Madre Oriental.

HÁBITAT: : Las poblaciones de esta especie se localizan entre 1125 y 1800 m de altitud, en zonas con selva mediana perennifolia, con presencia de arroyos permanentes y neblinas frecuentes durante todo el

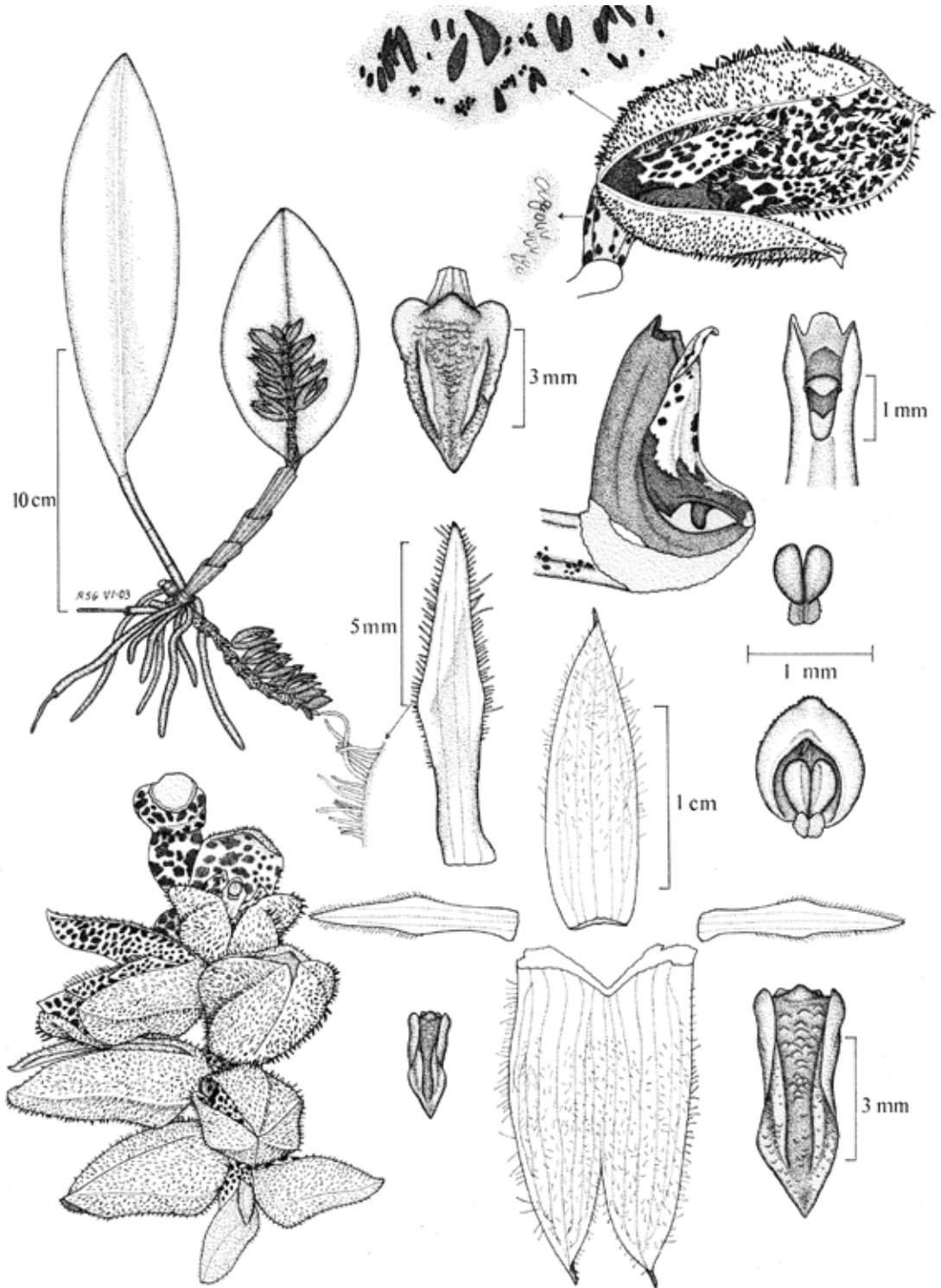


Figura 1. *Acianthera sotoana* R.Solano, basado en O. Suárez 566, (AMO, holo.), dibujo de R. Solano.

año. Las plantas crecen generalmente sobre rocas encima de una capa de musgo o materia orgánica, pero a veces también llegan a establecerse como epífitas. Las localidades de esta especie se conocen en zonas de clima semicálido húmedo, con un régimen de lluvias en verano, temperatura media anual de 18°C y precipitación superior a los 2000 mm al año.

FENOLOGÍA: Esta especie florece entre los meses de junio y septiembre, ha sido colectada con frutos en desarrollo en octubre y se han visto frutos secos poco después de haber liberado las semillas en marzo, época en la que empieza el crecimiento vegetativo.

ESTADO DE CONSERVACIÓN. No evaluado. Las poblaciones conocidas de esta especie se presentan dentro o en las inmediaciones de áreas naturales protegidas: el Parque Nacional Pico de Orizaba-Cofre de Perote (Veracruz), Reserva de la Biosfera Los Tuxtlas (Veracruz) y Reserva Comunal de Santa María Huitepec (Oaxaca), donde aún existe hábitat favorable para la orquídea.

ETIMOLOGÍA: Esta especie está dedicada a Miguel Ángel Soto Arenas, un maestro, amigo y colega para la mayoría de orquideólogos mexicanos en activo, por su invaluable aportación al estudio de las orquídeas mexicanas.

Esta especie, junto con *A. herrerae* (Luer) R.Solano & Soto Arenas y *A. johnsonii* forman un grupo que se caracteriza porque la inflorescencia surge de la base del tallo y de su ápice, el cual recientemente fue incluido, al igual que las especies de *Echinosepala* Pridgeon & M.W.Chase, en el género *Brenesia* Schltr. (Luer, 2004). Aunque los primeros ejemplares de *Acianthera sotoana* fueron colectados desde 1977, éstos fueron confundidos con *A. johnsonii*, una especie centroamericana que en México se conoce de la región de los Altos de Chiapas; sin embargo, la segunda es diferente por sus plantas de menor tamaño, flores más pequeñas, sépalos laterales más elípticos, pétalos más arqueados y el labelo con el ápice redondeado y el callo basal menos erecto (Solano Gómez & Soto Arenas, 2003). Por su parte, *A. herrerae* tiene sépalos con el mucrón más largo, pétalos abruptamente acuminados y atenuados, labelo con una forma muy diferente y provisto de lóbulos laterales uncinados (Luer, 1991, 2004). Previamente se había usado el nombre inédito “*Acianthera mixe*” para la especie aquí descrita y así

había sido registrada por algunos autores (Soto Arenas *et al.*, 2007; Solano Gómez *et al.*, 2008).

Stelis sotoarenasii R.Solano, *sp. nov.*

TIPO: MÉXICO. **Oaxaca:** Municipio Villa Sola de Vega, La Cumbre, carretera Oaxaca-Puerto Escondido, cerca de las torres de microondas, 2179 m, 16°27'12.32"N, 97°0'12.2"O, bosque de pino-encino, epífita en encino, abundante, 26 abril 2009, R. Solano 2550 (holotipo, OAX; isotipos, AMO, MEXU). FIG. 2, 3.

Stelis retusa (Ames) Pridgeon & M.W.Chase similaris sed folio latior ad apicem rotundato, racemis laxis, et floribus majoribus differt.

Hierba epífita, cespitosa, hasta de 14 cm de alto. *Raíces* 0.7-1.2 mm grosor. *Tallos* formados por 2 entrenudos, 2-6 cm largo, 1.0-1.5 mm diámetro, cubiertos totalmente por vainas tubulares, obtusas, carinadas y mucronadas, escariosas, caedizas; con un anillo engrosado cerca del ápice. *Hoja* una por tallo, apical, carnosa, erecta, oblanceolada, redondeada, ligeramente recurvada en el ápice, 3.5-9.5 x 1.3-1.8 cm, la base subpeciolada, atenuada, acanalada. *Inflorescencia* surgiendo del anillo del tallo, racemosa, más corta que la hoja, reclinada sobre la superficie foliar interna, 3-5 cm largo, con 4 a 8 flores que abren sucesivamente; pedúnculo, cilíndrico, 1.3-2.3 cm de largo, rodeado en la base por una bráctea espatácea, conduplicada, triangular, obtusa, escariosa; brácteas del pedúnculo 2, la basal cubierta por la bráctea espatácea, tubulares, oblicuas y obtusas en el ápice, membranáceas. *Brácteas florales* tubular-infundibuliformes, obtusas, cortamente apiculadas, membranáceas, 3.5-5.0 mm de largo. *Ovario* arqueado, ensanchado hacia el ápice, subtriangular en sección transversal, 4.3-4.9 mm largo; articulado a un pedicelo de 3.6-7.0 mm de largo. *Flores* bilabiadas, ligeramente colgantes, 9.0-9.5 mm de largo (de la base al ápice de los sépalos), 7.3-9.2 mm de apertura (entre el ápice del sépalo dorsal y los ápices de los laterales), 3.0-3.7 mm de ancho (entre los pétalos); los segmentos amarillos, densamente rayados y manchados de púrpura oscuro, columna blanca con manchas púrpura, antera amarilla con un mancha apical púrpura. *Sépalos* carnosos, 3-nervados; sépalo dorsal oblongo-lanceolado, obtuso, recurvado en el ápice, quillado en la superficie externa

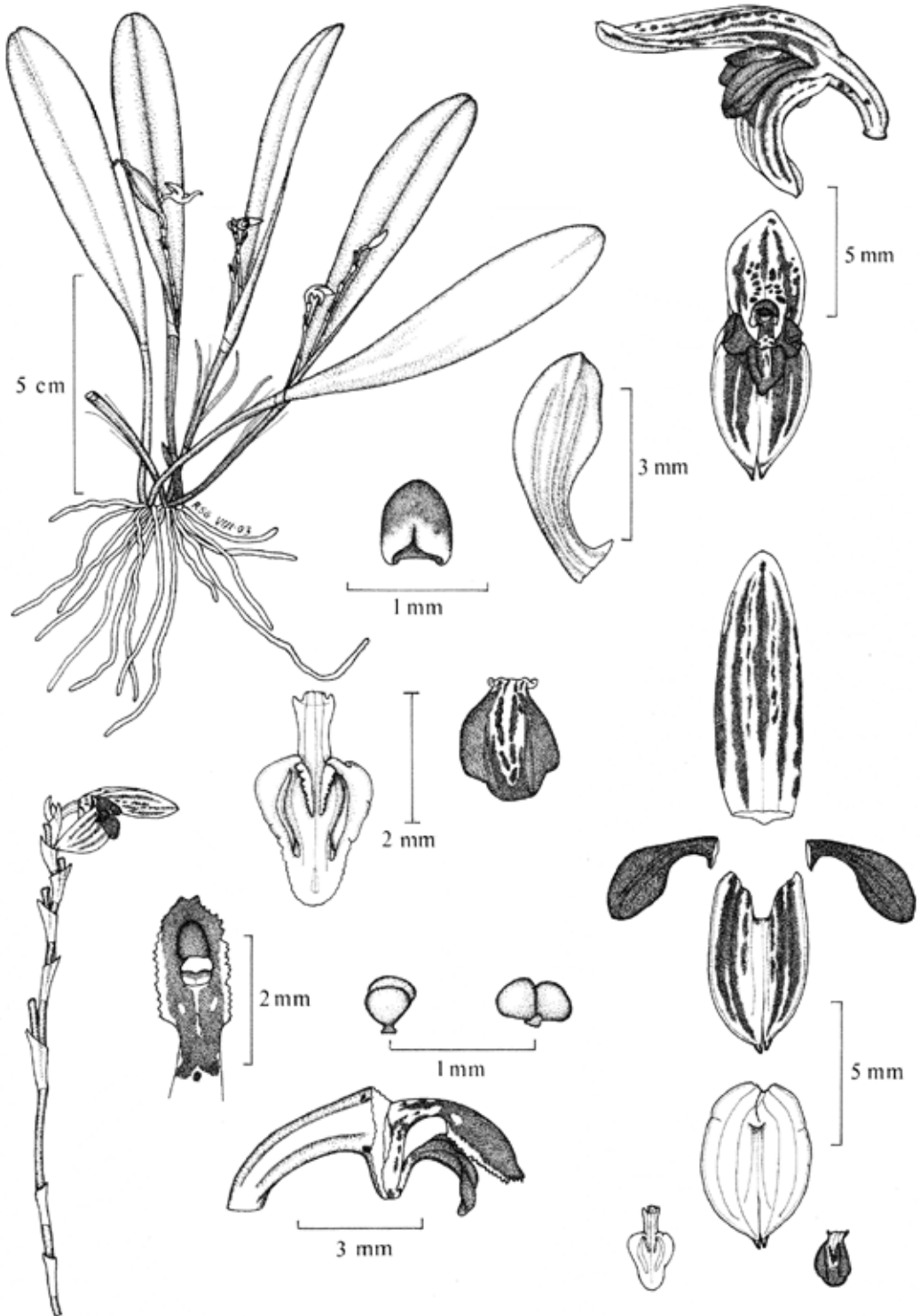


Figura 2. *Stelis sotoarenasii* R.Solano, basado en O. Suarez 2014, (AMO), dibujo de R. Solano.

a lo largo de la nervadura media, 9.0-9.4 x 3.0-3.4 mm; sépalos laterales connados por casi dos tercios de su longitud en un sinsépalo arqueado-recurvado, conduplicado, cortamente bilobado en el ápice, con la porciones libres adherentes, cuando extendido formando una lamina oval, obtusa, 5.5-6.0 x 3.3-3.5 mm; el ápice de cada sépalo cortamente apiculado. *Pétalos* erectos, cartilaginosos, falcado-espátulados, subredondeados, abruptamente atenuados en la mitad basal, 3-nervados, carinados en la superficie externa a lo largo de las nervaduras, 4.0-4.3 x 1.5-2.0 mm. *Labelo* provisto de una uña basal que se une al pie de columna, carnoso, arqueado-recurvado, conduplicado, 3-nervado, 1.8-2.0 x 1.3-1.5 mm en posición natural; la uña oblonga, 2-auriculada en la base, 1.0 x 0.6-0.8 mm; la lamina extendida ligeramente 3-lobada, obovada-subcordiforme, redondeada, 2.0-2.2 x 1.7 mm; con dos quillas erectas, prominentes que siguen el contorno de los márgenes y se extienden en los dos tercios basales de la lámina, mas otros dos callos internos más pequeños, crestados, lamelados, extendidos en el tercio basal de la lámina, aproximados en el ápice y divergentes hacia la base. *Columna* con un cuerpo delgado, fuertemente arqueado, alado, 3.5-3.6 mm de largo, 1 mm de ancho; provista de un pie prominente, descendente, ligeramente más corto que el cuerpo; clinandrio cubriendo totalmente la antera, con el margen denticulado; alas prominentes, proyectadas hacia el labelo, con el margen denticulado. *Estigma* ventral, cóncavo, subcuadrado, cubierto por una sustancia viscosa y transparente; rostelo ventral, laminar, convexo. *Antera* ventral, ovoide, 0.6 x 0.4 mm. *Polinario* formado por 2 polinios piriformes, lateralmente comprimidos, 0.35 mm de largo, provistos de caudículas granulosas.

OTROS ESPECÍMENES: MÉXICO. **Oaxaca:** Municipio Villa Sola de Vega, La Cumbre, carretera Oaxaca-Puerto Escondido, cerca de las torres de microondas, 2179 m, 16°27'12.32"N, 97°0'12.2"O, bosque de pino-encino, epífita en encino, *G. Cruz s.n.* (OAX). Abundante. Municipio San Juan Tepeuxila, camino Cuicatlán-Tlacolula, casi 4 km después de Tepeuxila, 2100 m, 17°43'47"N, 96°49'07"W, bosque de encino, epífita, 10 julio 2004, *R. Jiménez 2451, G. Salazar y J. Reyes* (AMO). Municipio Oaxaca de Juárez, Sierra de San Felipe, 17°4'N, 96°43'O, bosque de pino-encino, *O.*

Suárez s.n. (OAX). Municipio Villa Sola de Vega, km 90 de la carretera Oaxaca-Puerto Escondido, *O. Suárez* 2014, AMO. Municipio Villa Sola de Vega, km 114.7 de la carretera Oaxaca-Puerto Escondido, 2 noviembre 1974, *E. Greenwood s.n.* [AMO (diapositiva)].

DISTRIBUCIÓN. Esta especie es endémica de México y hasta ahora solo se conoce de las vertientes interiores de las Sierra Madre Oriental y la Sierra Madre del Sur en Oaxaca (FIG. 3).

HÁBITAT: Esta especie se encuentra entre 1500 y 2200 m de elevación, en bosques de encino y pino-encino con una estación de sequía bien marcada. Las plantas crecen como epífitas en troncos y ramas gruesas de encinos, directamente sobre la corteza o sobre una capa de musgo. Prospera en zonas de clima templado subhúmedo, donde las corrientes de viento son constantes y eso hace que no sean tan húmedos al interior.

FENOLOGÍA. En campo se han visto ejemplares de esta especie con flores desde abril, en cultivo la floración se extiende hasta octubre. No se han observado ejemplares con frutos desarrollados.

ESTATUS DE CONSERVACIÓN. No evaluado. Aunque solo una de sus localidades se presenta en un área protegida, la Reserva de la Biosfera Tehuacán-Cuicatlán, en las otras el hábitat es aún favorable y sus poblaciones pueden llegar a ser relativamente abundantes, formando en un solo árbol hospedero colonias integradas por hasta algunas decenas de individuos.

ETIMOLOGÍA. El nombre de esta especie honra a Miguel Ángel Soto Arenas por su excelente contribución al estudio de la taxonomía y conservación de las orquídeas mexicanas.

En el pasado esta especie ha sido confundida con *Stelis retusa*, considerándola como una forma geográficamente aislada de ésta. Sin embargo, *S. retusa* difiere en sus plantas de mayor tamaño, con hojas más angostas, racimo relativamente más florífero y los segmentos florales ligeramente más pequeños; se trata de una orquídea común en las montañas del centro y occidente de México, en el Eje Volcánico Transversal, mientras que *S. sotoarenasii* presenta una distribución restringida a Oaxaca. Otra especie muy similar es *S. aristocrática*, pero en esta las plantas son



Figura 3. Mapa mostrando la localización de las poblaciones conocidas de *Acianthera sotoana* R.Solano (triángulos) y *Stelis sotoarenasii* R.Solano (círculos).

más pequeñas, las hojas más anchas y espatuladas, los segmentos florales ligeramente más grandes y el sépalo dorsal no está recurvado; su distribución se restringe a la Sierra Madre del Sur en Guerrero. Para la especie aquí propuesta como *Stelis sotoarenasii* se había usado el nombre inédito “*Stelis zapotecana*”, con el cual fue citada por algunos autores recientemente (Soto-Arenas *et al.*, 2007; Solano Gómez & Soto Arenas, 2008; Solano Gómez *et al.*, 2008).

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**MASDEVALLIA SOTOANA (ORCHIDACEAE: PLEUROTHALLIDINAE),
A NEW SPECIES FROM ECUADOR**

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ABSTRACT: A new species of *Masdevallia*, *M. sotoana*, is described and illustrated from Ecuador. The new species is similar to *M. strobilii*, from which is mainly distinguished by the smaller size of the plant and flowers, the petals provided with a small basal teeth, the narrowly lanceolate lip abruptly reflexed at apex and the much shorter column foot.

RESUMEN: Se describe e ilustra una nueva especie de *Masdevallia* de Ecuador, *M. sotoana*. La nueva especie es similar a *M. strobilii*, de la cual se distingue especialmente por el tamaño menor de la planta y flores, los pétalos provistos con un pequeño diente basal, el labelo estrechamente lanceolado y abruptamente reflexo en el ápice, así como el pie de la columna mucho mas corto.

KEY WORDS: Orchidaceae, Malaxideae, *Crossoglossa*, *C. sotoana*, Costa Rica, new species

The genus *Masdevallia* Ruiz & Pav. includes today some 400 recognized species (Pridgeon, 2005) and more than 1100 published names (Tropicos, 2009). Although the genus has a long taxonomic history, with many species already known and cultivated during the 19th Century, the diversity of *Masdevallia* was substantially revealed in the last decades of the last Century, with a record of new descriptions between 1978 and 1988, when 265 *Masdevallia* names were proposed (references in Luer 1983—1988, 1996—2002, 1986a, 1986b, 2000a, 2000b, 2000c, 2001a, 2002, 2003). In the course of the actual decade, new species of *Masdevallia* appeared at a constant rate until 2005 (Königer 2000, 2001, 2003, Königer & Sijm 2003; Luer 2001b, 2001c, 2001d, 2002, 2004, 2005, Luer & Vásquez 2005, Ortiz 2004, 2005). Fewer taxa, however, have been published in the last few years (i.e., Luer & Dalström 2006, Wolff & Gruss 2007, Valenzuela 2008), with an average of only six new species per year since 2005 (compared with more than 14 species/year between 2000 and 2005). This may be in part the result of increasing difficulties in obtaining plant material from tropical countries, due to the enforcement of controls on wild plants trade, which particularly affect the interchange of samples

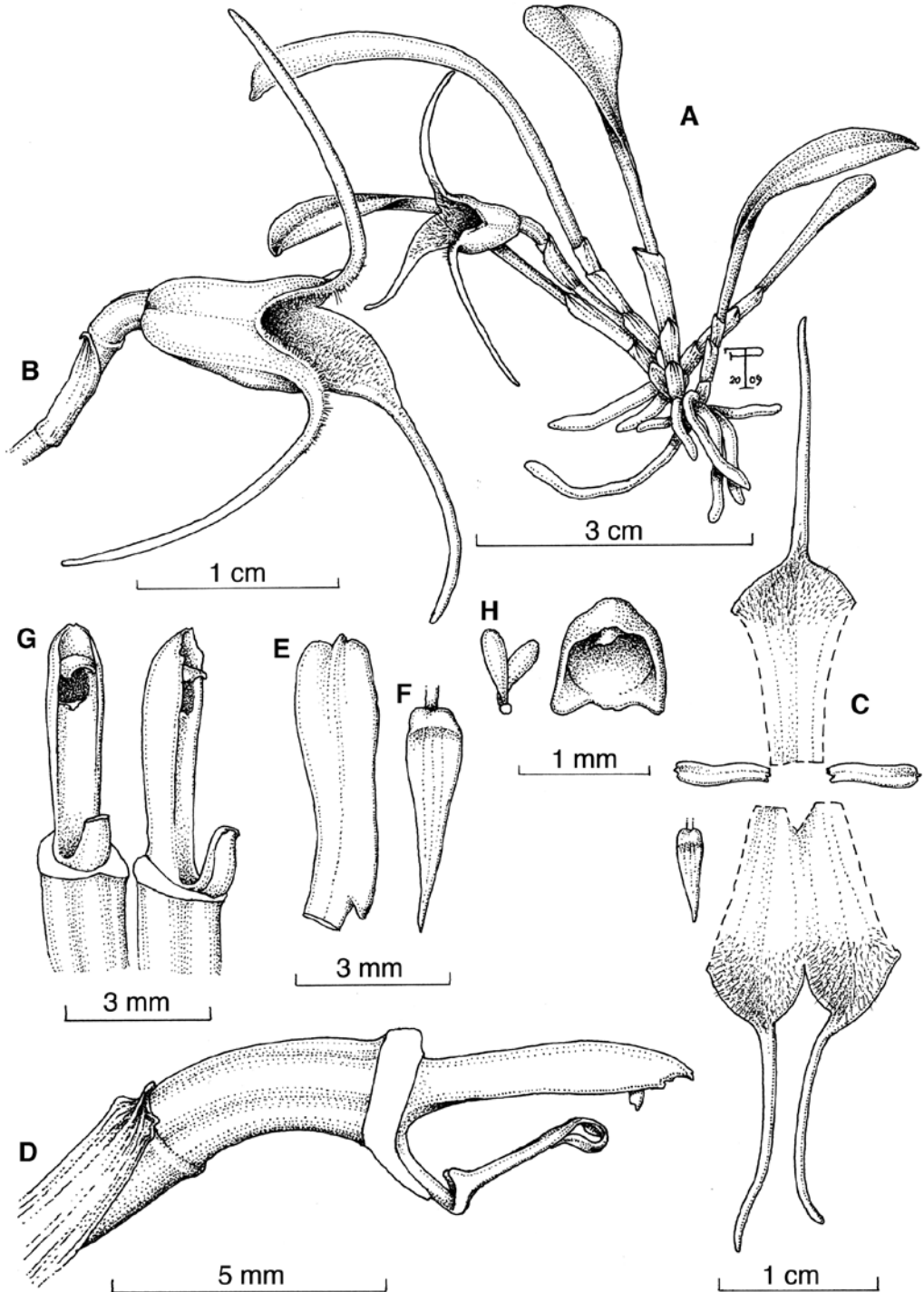
for scientific study. On the other side, it is likely that the big effort made by Luer and his co-workers in the last 30 years to illustrate the diversity of *Masdevallia* is approaching completeness, significantly reducing the number of new findings in this group of plants.

During the process of reviewing the taxonomic identity of the vast *Masdevallia* collection at Ecuagenera, to be documented and incorporated as scientific reference in the living orchid collection of the Andean Orchid Research Center (CIOA, for its acronym in Spanish), University Alfredo Pérez Guerrero, and in the related databases, we found a number of taxa that do not fit well in any of the previously described species. The new species proposed here has apparently no close relatives, with the exception of *M. strobilii* Sweet & Garay, and we confidently described it as:

Masdevallia sotoana H. Medina & Pupulin, *sp. nov.*

TYPE: Ecuador. Zamora-Chinchipe: near The Tambo, 1800 m, November 1993, flowered in cultivation in the collection of Ecuagenera at Gualaceo, accesión No. 002293, 14 Oct. 2009, *H. Medina 72* (holotype, QCNE). Fig. 1—2.

Masdevalliae strobilii Sweet et Garay similis, foliis minoribus acutis, floribus multo minoribus, sepalibus



Masdevallia sotoana Pupulin & H.Medina. A — Habit. B — Flower. C — Dissected perianth. D — Pedicel, ovary, column and lip, lateral view. E — Left petal. F — Lip, spread. G — Column, ventral and three quarters views. H — Pollinarium and anther cap. Drawn by F. Pupulin from the holotype.

trichomatibus parvibus ornatis, petalis lineari-oblongis dente basali perparvo instructis, labello anguste lanceolato acuminato, apice abrupte reflexo, pede columnae multo brevior recedit.

Epiphytic, caespitose, erect *herb*, to 7 cm tall. *Roots* filiform, flexuous, ca. 1 mm in diameter. *Stems* (ramicauls) shorter than the leaf, erect, ca. 5 mm long, concealed by 2–3 tubular, loose, scarious sheaths, 3–8 mm long. *Leaves* petiolate, the blade elliptic, acute, minutely tridenticulate, green, the base of the petiole darker, 2.8–3.5 x 1.0–1.2 cm; petiole conduplicate, to 2.4 cm long. *Inflorescence* single-flowered, erect, slender, terete, produced laterally from the apex of the stem, to 3.5 cm long. *Floral bract* tubular-lanceolate, amplexent, glumaceous when young, becoming dry-papyraceous with age, 6 mm long. *Pedicel* terete, to 6 mm long. *Ovary* articulated with the pedicel, terete, glabrous, 4 mm long. *Flowers* forming a sepaline cup and apically spreading into long tails, white, flushed orange-yellow toward the base, the apical tails yellow, the petals, the lip and the column white. *Sepals* united to form a tube, ventrally slightly gibbous, minutely papillose-hirsute toward the apex of the blade, 3-nerved, abaxially carinate along the midnerve, 1.4 cm long, each 6 mm wide, basally connate for ca 1.1 cm, the free portion semi-rounded to transversely elliptic, extending at apex into a narrow, filiform tail 1.5 cm long. *Petals* linear-oblong, slightly sygmoid, minutely tri-dentate, 1-nerved, the lower margin produced at the base into a short, triangular teeth, thickened along the nerve, 5.0 x 1.7 mm. *Lip* narrowly lanceolate, acuminate, subtruncate-bilobed at base, the margins of the basal lobes suberect, apically abruptly reflexed, 4.5 x 1.2 mm. *Column* straight, 5 mm long, with low marginal wings increasing toward the apex to form a hood over the clinandrium; anther ventral, stigma elliptic. *Pollinia* 2, narrowly oblong, on a rounded viscidium.

PARATYPE: Ecuador. Same locality as the holotype, November 1993, flowered in cultivation in the collection of Ecuagenera at Gualaceo, accession No. 001094, 19 Aug. 2008, *H. Medina 69* (QCA).

EPONYMY: Dedicated to Miguel Angel Soto Arenas, for his outstanding contributions to the study and knowledge of Neotropical orchids.

DISTRIBUTION AND ECOLOGY: Know only from southeastern Ecuador. A single population of this species has been found in the submontane wet forests of the Province of Zamora-Chinchipe, growing at about 1800 meters of elevation.

According to Luer's (2002) scheme of subgeneric classification, *M. sotoana* belongs to subgen. *Masdevallia* sect. *Masdevallia* subsect. *Saltatrices* (Rchb.f.) Luer. The group was not affected by generic recircumscriptions and nomenclatural changes recently proposed by Luer (2006) in his reconsideration of *Masdevallia*. *Masdevallia* subsect. *Saltatrices*, which is distributed in the Andes from Venezuela into Peru, is mostly characterized by the deeply connate sepals into a sepaline tube that is often, but not always ventricose (Luer 1996, 2002). The subsection includes 26 species, some of them not closely related. As Luer (2002) himself recognizes, the distinction between subsections *Saltatrices* and *Masdevallia* is not sharp.

Among the taxa of subsect. *Saltatrices*, *M. sotoana* has apparently only a single close relative, *M. strobilii*. This species was first discovered in the province of Zamora-Cinchipe in southeastern Ecuador by Calaway H. Dodson and independently collected in the same region by José Strobel (Sweet & Garay 1966). In this region, *M. sotoana* and *M. strobilii* are sympatric. *Masdevallia sotoana* may be distinguished from *M. strobilii* by the smaller size of the plant (leaves 2.8–3.5 vs. 4–6 cm in *M. strobilii*) and the flowers (sepals <3 cm vs. >5 cm), the petals provided with a small basal teeth (0.5 mm vs. 2 mm), the narrowly lanceolate lip (vs. obovate) abruptly reflexed at apex (vs. arcuate) and the much shorter column foot (2 mm vs. 5 mm).

ACKNOWLEDGEMENTS. We would like to express our most sincere tanks to José "Pepe" Portilla and his family for allowing us free access to the plant collection of Ecuagenera and giving any kind of facilities. To the Ministry of Environment of Ecuador for extending the management permits of the living collections where the species treated here have been documented. To the Foundation for Orchid Research and Conservation, Vancouver Orchid Society, Canada, for its kind sponsoring of the AORC. The present paper is part of the Project 814-A7-015, "Inventario y taxonomía de la flora epífita de la región Neotropical — Orchidaceae", sponsored by the Vice-Presidency of Research, University of Costa Rica.

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NEW SPECIES OF *PORROGLOSSUM* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM ECUADOR

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ABSTRACT. Three new species of *Porroglossum* from Ecuador are described and illustrated. *Porroglossum miguelangelii* is compared to the Peruvian *P. lycinum*, from which it differs by the longer, narrower petals with margins that are not obtusely angled below the middle and the presence of stigmatic tooth-like processes. *Porroglossum merinoi* is distinctive in that it is the only species with densely pubescent sepals. *Porroglossum porphyreum* is similar to *P. schramii*, but differs in the sepals with a thickened tail abruptly inserted at their apex, the petals with teeth on both the upper and lower margin, and the labellum provided with a longer and broader basal callus.

KEW WORDS: Orchidaceae, Pleurothallidinae, *Porroglossum*, *P. miguelangelii*, *P. merinoi*, *P. porphyreum*, Ecuador, new species

Introduction. The genus *Porroglossum* Schltr. (Orchidaceae) includes 38 species restricted to Andean South America, where they range from Venezuela to Peru (Luer 1987). Ecuador is the genus's center of diversity with 23 species recorded (Dodson 2004). With 8 species, Colombia has the second highest species concentration. The first species described, *Porroglossum echidna* (Rchb.f.) Garay, was discovered in Colombia and was attributed to the genus *Masdevallia* Ruiz & Pav. based on its caespitose habit, short ramicauls, and sepals with long tails (Luer 1987). Rudolf Schlechter proposed the genus in 1920, based on *P. colombianum* [= *P. mordax* (Rchb.f.) Sweet] and *P. muscosum* (Rchb.f.) Schltr., mainly distinguishing *Porroglossum* from *Masdevallia* by the apical position of the anther and the presence of a long column foot with a free apex (Schlechter 1920). The unusually long column foot in *Porroglossum* functions to accommodate the active mobility of the labellum. The region of the labellum that rests against the

column foot is sensitive to tactile stimuli and responds to touch by relaxing the labellum's long strap-like claw. This allows the labellum to reflex backwards and (hypothetically) push the pollinator against the column (Bean 1887, Leavitt 1906, Luer 1987). Although the pollination system has been described in detail by Bean (1887), Oliver (1888) and Luer (1987), the specific pollinators and mechanism of the genus has not yet been recorded in nature.

Sensitive labella have evolved independently in other taxa of the subtribe Pleurothallidinae Lindl. (Luer 1987, 2000). Examples include *Acostaea* Schltr. and *Condylago* Luer species, now treated as members of the genus *Specklinia* Lindl., and *Masdevallia teaguei* Luer, which was once recognized as the monotypic genus *Jostia* Luer. The presence of an irritable lip was once thought to be a key character for generic circumscription. Recent phylogenetic analyses based on combined molecular evidence (Pridgeon *et al.* 2001) show that in some cases it is unsuitable as a character for generic

circumscription within the Pleurothallidinae because it creates paraphyletic groups. In contrast, lip motility observed in the well supported monophyletic clade of *Porroglossum* can be considered a synapomorphy of the genus. *Porroglossum* is the only currently accepted and recognized genus in the Pleurothallidinae that can be characterized as a whole by the presence of actively motile labella.

The systematics of *Porroglossum* was treated by Sweet (1970, 1972) and by Luer (1987). Luer recognizes two subgenera, subgen. *Eduardia* Luer and subgen. *Porroglossum*. Subgenus *Eduardia* is characterized by a repent growth habit and a simultaneously flowered inflorescence. The subgenus *Porroglossum* is composed of three sections: section *Echidnae* (Rchb.f.) Luer which contains species characterized by peduncle indumentums, section *Tortae* Luer which contains species characterized by non-resupinate flowers, and section *Porroglossum* which contains the rest of the species (Luer 1987). The species described here all belong to the section *Porroglossum*.

Luer (1987) attributed twenty-seven species names to the genus *Porroglossum*, considering *P. colombianum* and *P. xiphères* to be synonyms of *P. mordax* and *P. muscosum*, respectively. Since then, Luer has authored and co-authored thirteen new species, bringing the number of species names attributed to *Porroglossum* to forty and the number of species to thirty-eight (Luer 1988, 1989, 1991, 1994, 1995, 1998, 2004, 2006a, 2006b). In Ecuador, 23 species of *Porroglossum* have been previously recorded, representing over two thirds of the known species. In preparing a systematic revision of the Ecuadorian species of *Porroglossum*, we found three species that present enough morphological differences from the previously described species to be confidently proposed as new to science.

Porroglossum miguelangelii G.Merino, A.Doucette & Pupulin, *sp. nov.*

TYPE: Ecuador. Zamora Chinchipe: without specific locality, 1800 m, collected by Hugo Medina, November 1993, cultivated by Ecuagenera Orchid Nursery in Gualaceo, flowered in cultivation, 20 July 2008, *G. Merino 1* (holotype: QCNE; isotype: Andean Orchids Research Center (CIOA, by the initials in

Spanish), University Alfredo Pérez Guerrero, Spirit Collection No. 000845). FIG. 1, 4A.

A Porroglosso procul Luer foliis ellipticis obtusis, petalis lineari-ligulatis subfalcatis, in parte media leviter angustatis, lamina labelli late obtriangulari-obcuneata marginibus lateralibus incurvatis recedit.

Herb epiphytic, caespitose, 4 to 8 cm tall. *Roots* flexuous, 1 mm in diameter. *Ramicauls* terete, erect, abbreviated, blackish at the base 1 mm long, enclosed by 2 to 3 tubular sheaths. *Leaf* coriaceous, spatulate, elliptical-obovate 2-4 x 0.5-1.0 cm, narrowed at the base into a conduplicate petiole 1.5-2.0 cm long. *Inflorescence* a congested, successively flowered raceme 8-10 cm long; the peduncle glabrous, 5.0-9.5 cm long. *Floral bracts* tubular, 4 mm long. *Pedice*l 5 mm long. *Ovary* terete, minutely verrucose, 6-sulcate, 5 mm long. *Flowers* resupinate, held erect, without a detectable fragrance, the dorsal sepal yellow-green suffused with brown, with three brown veins, the lateral sepals yellow-green, the petals translucent, amber with a brown mid-vein, the lip white, spotted with dark brown, the column greenish-white with a cream anther cap. *Dorsal sepal* broadly ovate, concave, tricarinate, 9.5-10.0 x 5.0 mm, contracted into a thick, erect tail, connate to lateral sepals for about 3 mm. *Lateral sepals* subrectangular, tricarinate, 10-11 x 6 mm when spread, connate for about 4 mm to form a laterally compressed cup, contracted at apex into a thickened, horizontally outstretched tails. *Petals* linear-ligulate, the apex rounded and broader than middle portion, 6 x 1 mm. *Lip* unlobed, obcuneate-obtriangular, 4 x 5 mm at its widest portion, hinged to the column foot by a short rectangular strap, motile, with a sulcus running from the apex to the center of the blade, with a basal low, broad callus. *Column* short, stout, semiterete, fleshy, to 3 mm long, with two tooth like processes near the stigma. *Anther cap* transversely ovate, obtuse-apiculate. *Pollinia* droplet shaped, 2 in number, each with a glandular caudicle.

EPONYMY: Named to the memory of Miguel Ángel Soto Arenas, in recognition of his outstanding contributions to the knowledge of orchids.

DISTRIBUTION: Known only from southeastern Ecuador.

HABITAT AND ECOLOGY: Epiphytic in shade in premontane and lower montane cloud forests, usually

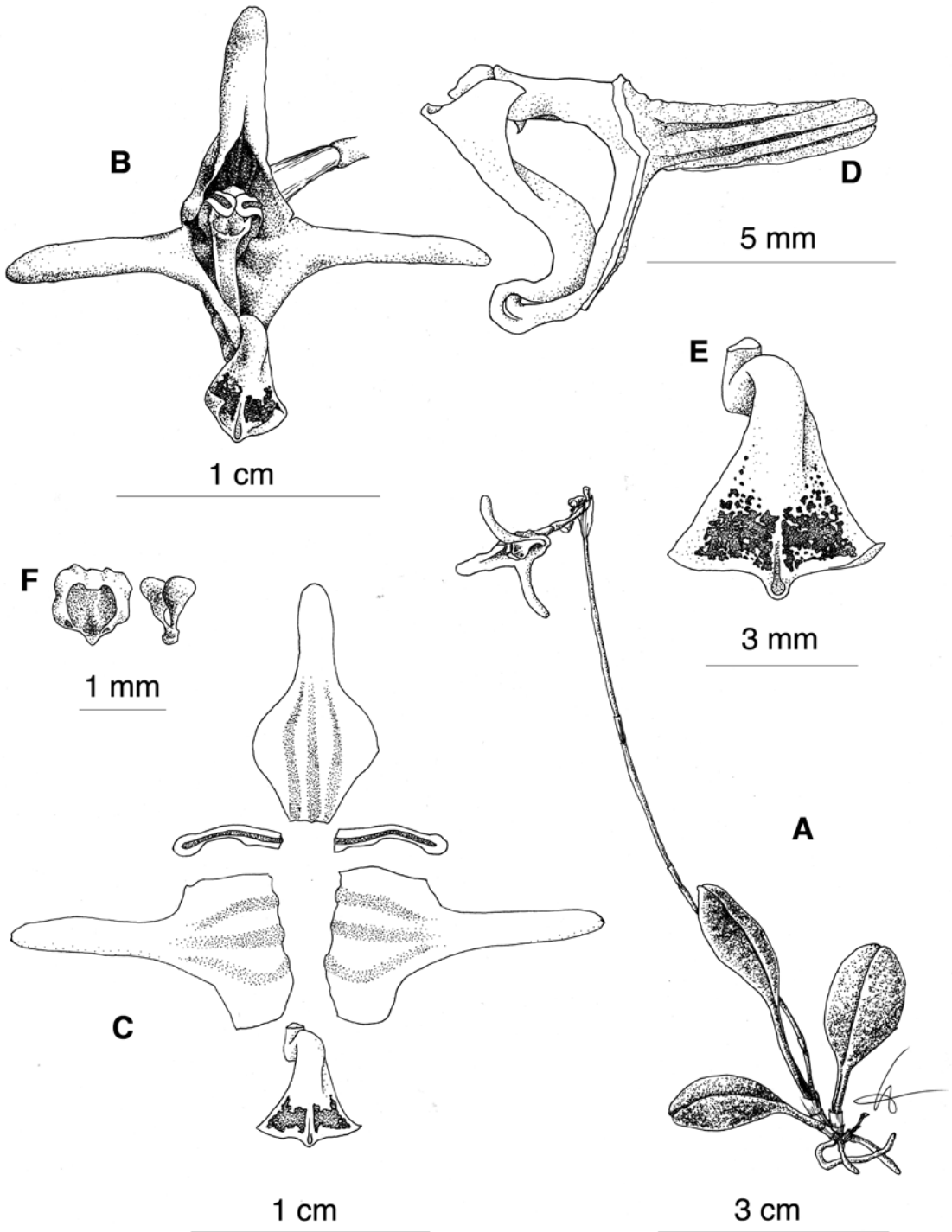


FIGURE 1. *Porroglossum miguelangelii* G.Merino, A.Doucette & Pupulin. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip, spread. F — Anther cap and pollinarium. Drawn by A. Doucette from the holotype.

in windy areas, at elevations of 1800 meters, where the plants mostly establish on small trees covered by mosses and lichens.

Porroglossum miguelangelii is most similar to *P. lycinum* Luer from northern Peru, from which it differs by smaller plants, the longer, narrower petals with margins that are not obtusely angled below the middle, the presence of tooth-like processes before the stigma (absent in *P. lycinum*), the spreading, pale green sepals, suffused with yellow at their apices (vs. projected forwards, speckled and suffused with brown in *P. lycinum*). The two species have similarly shaped labella that are both pale green and heavily flecked with dark purple towards their apex.

Porroglossum merinoi Pupulin & A. Doucette, *sp. nov.*

TYPE: ECUADOR. Morona-Santiago: Tumbes, 1200 m, collected by Gilberto Merino, October 1993, flowered in cultivation, 12 June 2007, *G. Merino* 2 (holotype: QCNE; isotype: CIOA, Spirit Collection No. 000155). FIG. 2, 4B.

Species Porroglossum lycino Luer *similis*, *floribus expansis sepalo superno reflexo, caudis sepalorum brevioribus ligulato-rotundatis, petalis ligulatis dente triangulari margine infero instructis, labello obrullato obtuso glabro differt.*

Herb epiphytic, caespitose, to 6 cm tall. *Roots* flexuous, 1 mm diameter. *Ramicauls* erect, slender, 10--12 mm long, enclosed by 2 to 3 tubular, membraneous sheaths that become papery with age. *Leaf* erect, coriaceous, long-petiolate, the blade elliptic-oblanceolate, sub-verrucose, 2.5-3.0 x 0.7-1.0 cm, narrowed at the base into a conduplicate petiole 2.6-3.0 cm long. *Inflorescence* a suberect, congested, successively few-flowered raceme to 15 cm long; the peduncle terete, slender, glabrous, provided with 4-5 widely spaced, tubular bracts to 7 mm long. *Floral bract* tubular, 5 mm long. *Pedicel* terete, 7-8 mm long. *Ovary* terete, subverrucose, 5 mm long. *Flowers* resupinate, partially spreading, lightly fragrant of cloves, the sepals greenish yellow, pubescent, flushed with solid yellow at the glabrous apexes, the nerves yellow, the dorsal sepal with a central, purplish flush at the base; the petals translucent yellowish white, with a central stripe and the apex purple-red; the lip

yellow, finely spotted with red; the column purple, with a yellowish white anther cap. *Dorsal sepal* lanceolate, narrowly obtuse, tricarinate, concave at the base, parallel to the column below the middle and gently deflexed above the middle, 6 x 3 mm, connate to the lateral sepals for about 1.5 mm to form a slightly, laterally-compressed cup. *Lateral sepals* transversely obtapezoidal, 3-veined, narrowed at the middle into thick, ligulate, narrowly obtuse-rounded, forwardly directed tails, 7.5 mm long x 8 mm at its widest portion when spread, basally connate for about 1.5 mm to the dorsal sepal, connate to each other and to the column foot about 5 mm to form a deep, subacute, rounded chin. *Petals* subfalcate, 1-nerved, the lower margin with a triangular tooth below the middle, rounded at apex 4.0 x 1.3 mm, *Lip* long-unguiculate, the blade obcuneate-spathulate, broadly obtuse, with a short, sulcate, rounded apiculum, 5.5 mm long x 3 mm at its widest portion, thickened at the base into the straplike claw, bent with tension toward the free apex of the column-foot. *Column* semiterete, truncate, 2.5 mm long, with narrowly triangular-subfalcate, descending substigmatic arms, produced at the base into a slender, curved foot about 6 mm long; the anther terminal, incumbent. *Anther cap* transversely ovate, obtuse-apiculate. *Pollinia* droplet shaped, 2 in number, each with a glandular caudicle.

EPONYMY: Named after Gilberto Merino, Ecuadorean orchid researcher with a strong interest in Pleurothallidinae, who first collected this species.

DISTRIBUTION: Collected once, known only from southeastern Ecuador.

HABITAT AND ECOLOGY: The type specimen of *P. merinoi* was found growing as a shade epiphyte on a small tree covered by mosses, in cloud forest at about 1800 m of elevation. In cultivation, it flowers from May to June.

Porroglossum merinoi is one of the most distinctive species in the genus. It is the only species with truly pubescent sepals. *P. hirtzii* bears minute hairs on its sepals but they are sparsely distributed. *P. merinoi* is allied to *P. andreettae*, from which it differs by the petals with entire margins (vs. contracted into acute apices near the middle), a slightly broader labellum, and puberulent sepals provided with a thickened, glabrous, yellow apex. Both species are lightly fragrant.

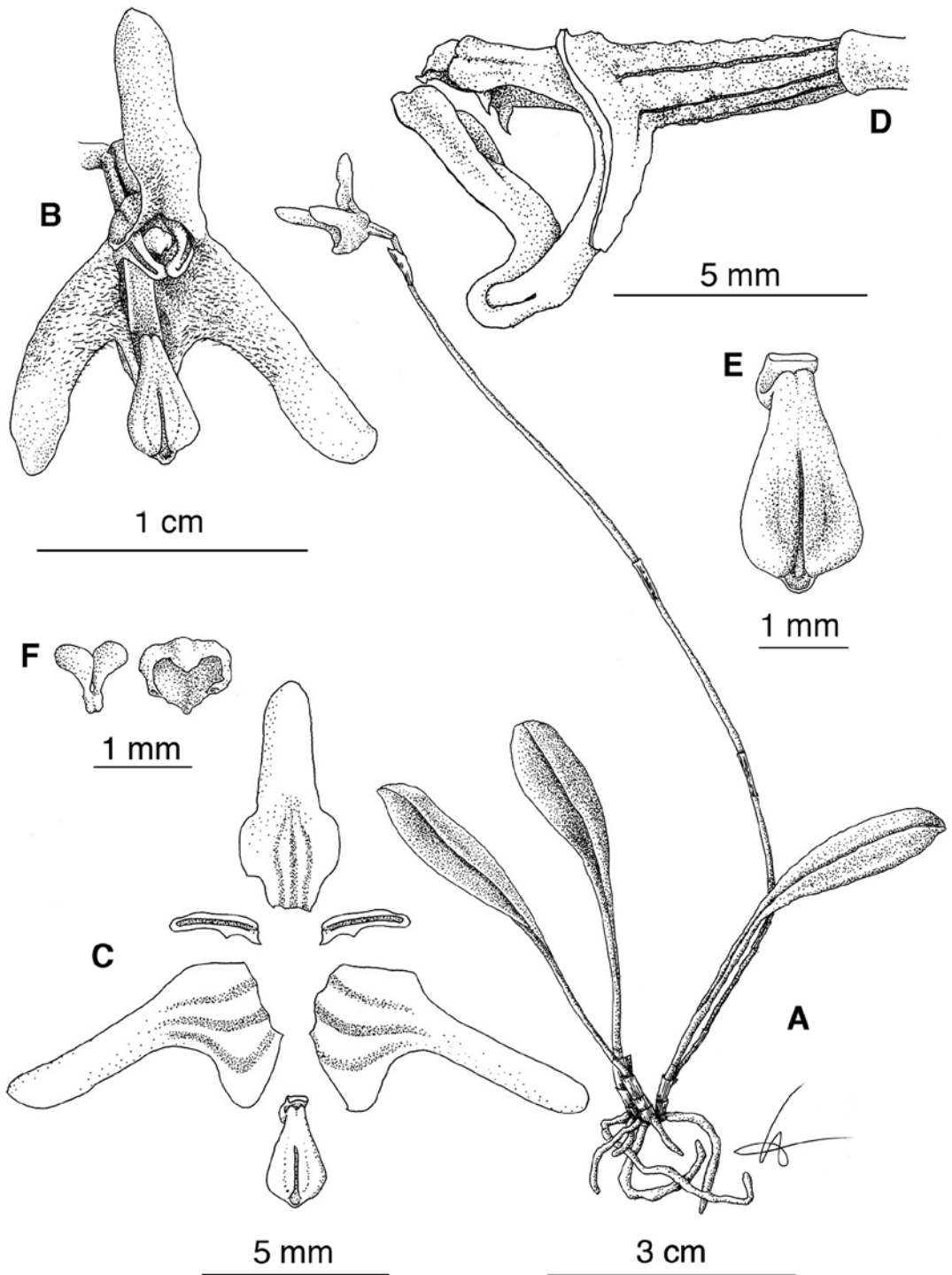


FIGURE 2. *Porroglossum merinoi* Pupulin & A.Doucette. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip, spread. F — Pollinarium and anther cap. Drawn by A. Doucette from the holotype.

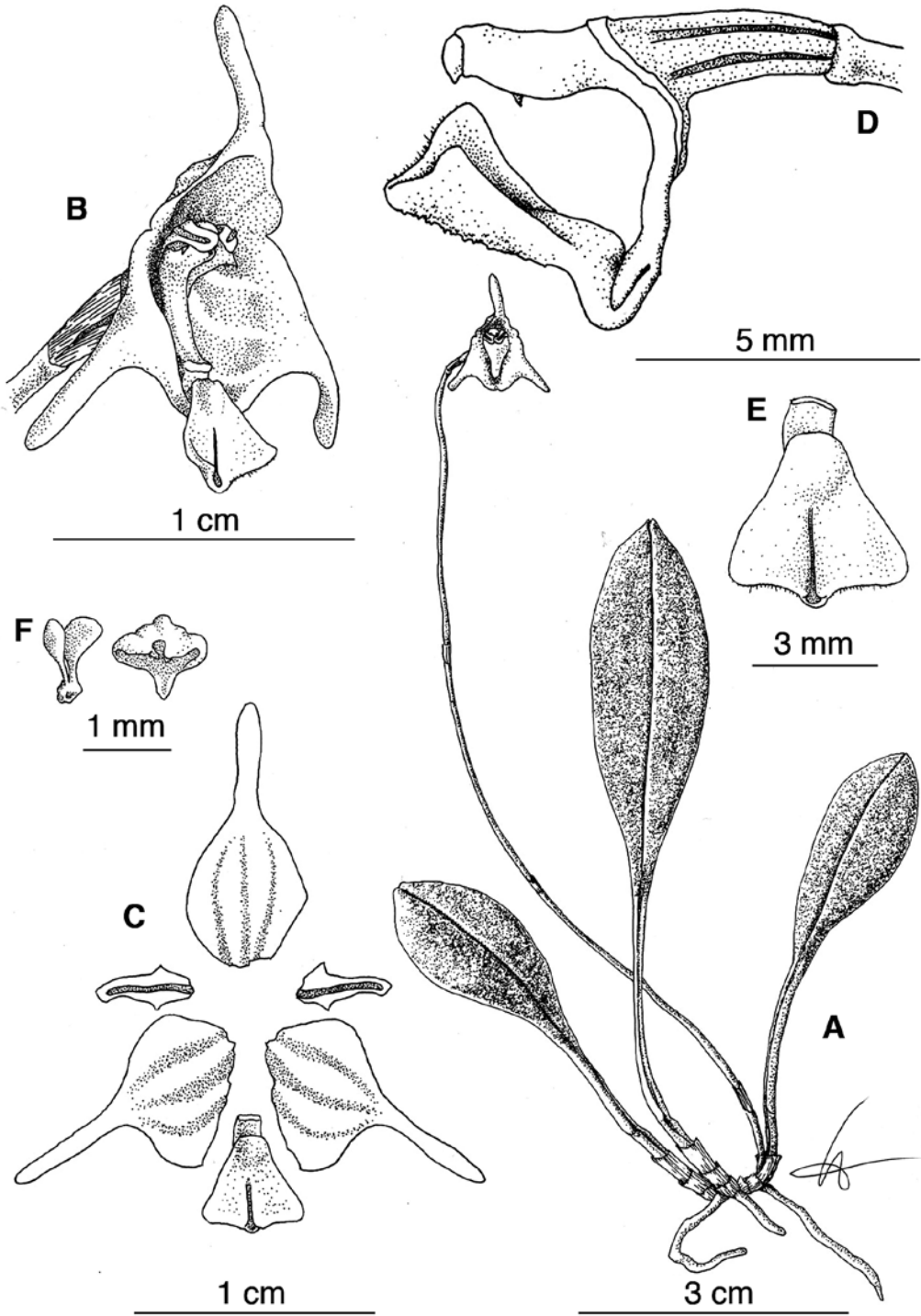


FIGURE 3. *Porroglossum porphyreum* G.Merino, A.Doucette & Pupulin. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Lip, spread. F — Pollinarium and anther cap. Drawn by A. Doucette from the holotype.

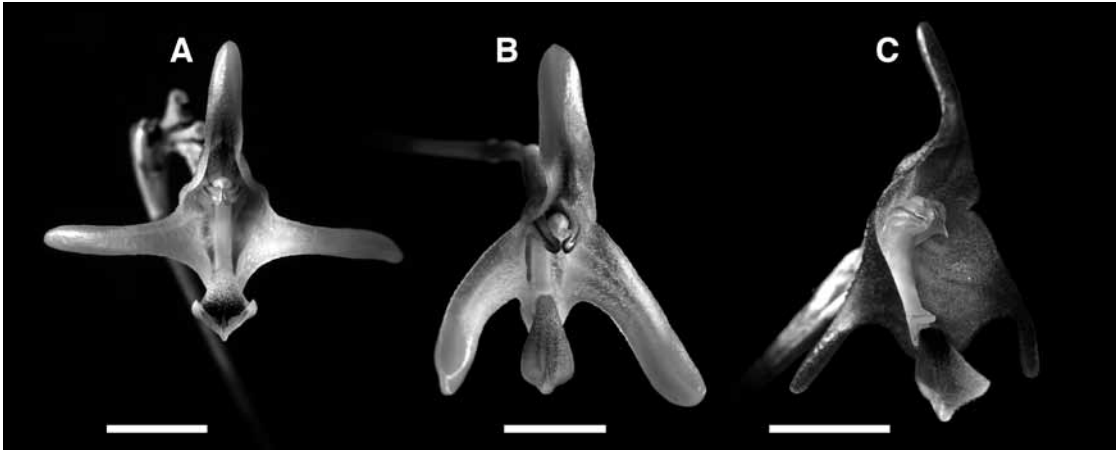


FIGURE 4. Pictures of holotype flowers of three new *Porroglossum* species. A — *Porroglossum miguelangelii*.. B — *P. merinoi*. C — *P. porphyreum*. Scale bars = 5 mm. Photographs by F. Pupulin.

Porroglossum porphyreum G.Merino, A.Doucette & Pupulin, *sp. nov.*

TYPE: ECUADOR. Morona-Santiago: El Aguacate, 1600 m, collected by Jinsop Medina, 1992, cultivated by Ecuagenera Orchid Nursery in Gualaceo, flowered in cultivation, 20 July 2008, *G. Merino* 3 (holotype: QCNE; isotype: CIOA, Spirit Collection No. 000743). FIG. 3, 4C.

A Porroglossos schramii Luer *caudis sepalorum brevioribus incrassatis, sepalis lateralibus transverse ellipticis cauda apicali abrupte instructis, petalis dente acuto margo inferno munitis, labello toto dense pubescenti callo basali magno latiore recedit.*

Herb epiphytic, caespitose. 6 to 10 cm tall. *Roots* flexuous, 1 mm in diameter. *Ramicauls* terete, erect, abbreviated, blackish at the base, 3--5 mm long, enclosed by 2 to 3 tubular, membraenous sheaths that become papery with age. *Leaf* coriaceous, elliptic-obovate, obtuse to acute, 3-5 x 1.5-2.0 cm, narrowed at the base into a conduplicate petiole 1--3 cm long. *Inflorescence* a congested, successively, few flowered raceme; the peduncle terete, slender, glabrous, 10-12 cm long. *Floral bract* tubular, 4mm long. *Pedicel* 5 mm long. *Ovary* terete, minutely verrucose, 6-sulcate, 6 mm long. *Flowers* resupinate, held erect to horizontally, without apparent fragrance, the sepals yellowish white heavily suffused with purple, the petals amber with a brown mid-vein, the lip white suffused with purple, the

column and the anther cap white. *Dorsal sepal* ovate, acute, concave, tricarinate, 6 x 3 mm, contracted at apex into an erect to forward projecting, thickened, linear tail, connate to lateral sepals for about 4 mm, the tails 1 mm in diameter. *Lateral sepals* ovate, slightly compressed, tricarinate, 10 x 5 mm wide when spread, connate at the base for about 7 mm, abruptly contracted at apex into thickened tails that may project forwards or slightly reflex backwards. *Petals* subfalcate, truncate, 4 x 2 mm, the margins present two triangular teeth below the middle. *Lip* entire, obcuneate, 4 x 5 mm at its widest portion, hinged by a short rectangular strap to the column foot, motile, microscopically pubescent, with a sulcus running from the apex to the center of the lip, the base with a low, broad callus. *Column* short, stout, semiterete, fleshy, 3 mm long, with two tooth-like processes close to the stigma. *Anther cap* transversely ovate, obtuse-apiculate. *Pollinia* droplet shaped, 2 in number, each with a glandular caudicle.

PARATYPES: Same locality as the holotype, flowered in cultivation at Ecuagenera Orchid Nursery in Gualaceo, 10 December 2008, accession No. CIOA-001373 (Centro de Investigación en Orquídeas de los Andes-Spirit); accession No. CIOA-001374 (Centro de Investigación en Orquídeas de los Andes-Spirit).

ETYMOLOGY: From the Greek *porphyreos*, purple, in allusion to the color of the flower.

DISTRIBUTION: Known only from southeastern Ecuador.

HABITAT AND ECOLOGY: Plants of *P. porphyreum* grow as shade epiphytes on the moss covered branches of shrubs, in the premontane forests of southern Andean Ecuador. In its natural habitat, *P. porphyreum* has been observed in flower from March to July; plants in cultivation flower most of the year.

Porroglossum porphyreum is similar to *P. schramii* Luer. *P. porphyreum* can be distinguished from *P. schramii* by having sepals that abruptly (rather than gradually) contract into thickened (rather than thin) sepaline tails. The petals of *P. porphyreum* have teeth below the middle on both margins while the petals of *P. schramii* only bear a tooth margin on the upper margin. The labellum of *P. porphyreum* has a basal callus that is longer and broader than the basal callus of *P. schramii*.

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ON THE IDENTITY OF *MYOXANTHUS SCANDENS* (ORCHIDACEAE: PLEUROTHALLIDINAE), WITH A NEW SPECIES FROM COSTA RICA

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ABSTRACT: We present and illustrate a new species of *Myoxanthus* from Costa Rica, closely related to *M. scandens*. We present descriptions and illustrations of both species. The new species, *Myoxanthus sotoanum* differs from *M. scandens*, by its linear leaves, the brownish-yellowish flowers, the yellow petals and lip, the oblong, obtuse, subfalcate lateral lobes of the lip, the two keels extending nearly to the middle of the lip, and the shorter, triangular, acute teeth that flank the stigma. *Myoxanthus sotoanum* generally also occurs at lower elevations than *M. scandens*.

RESUMEN: Presentamos e ilustramos una nueva especie de *Myoxanthus* para Costa Rica, junto a la descripción e ilustración de *M. scandens* basadas en material costarricense. La nueva especie, *Myoxanthus sotoanum*, es similar a *M. scandens*, de la que difiere principalmente por sus hojas lineares, las flores café-amarillento, los pétalos y el labelo amarillos, los lóbulos laterales del labelo oblongos, obtusos y subfalcados, las dos quillas que se extienden hasta la mitad del labelo y los dientes más cortos, triangulares, agudos, que flanquean el estigma. *Myoxanthus sotoanum* generalmente se encuentra a elevaciones inferiores que *M. scandens*.

KEY WORDS: *Myoxanthus scandens*, Costa Rica, *Myoxanthus sotoanum*, new species, Orchidaceae

Members of the subtribe Pleurothallidinae (Orchidaceae) are often taxonomically problematic. Both in herbaria and living collections, names of Pleurothallidinae are frequently applied without direct knowledge of the nomenclatural types. Moreover, the general overall similarity in the flowers of some groups and their usually reduced dimensions make more difficult a careful comparison between closely related taxa. The misunderstanding of the critical characters that allow taxonomic identification, the particular species concept used and an insufficient appreciation of natural variation, often lead to incorrect species circumscriptions. Under these circumstances, it is possible that undescribed species remain hidden under broadly defined taxonomical concepts.

In Costa Rica, the plants identified as *Myoxanthus scandens* Ames (Luer) are likely a fine example of this problem [Atwood, 1987, 1989 (both with illustration); Pupulin, 2002; Luer, 1976, 1982, 1992, 2003]. This species is member of a small group of *Myoxanthus* species characterized by the prolific, usually pendent

stems, and mostly narrowly elliptic leaves, including *M. chloë* (Luer & Vásquez) Luer, *M. epibator* Luer & Escobar, *M. fimbriatus* Luer & Hirtz, *M. frutex* (Schltr.) Luer, *M. parvilabius* (C. Schweinf.) Luer, and *Pleurothallis pennellia* Luer. With the exception of *M. scandens*, which ranges northward to Costa Rica, this group is eminently South American in distribution, with the highest diversity in the Andes from Colombia to Bolivia. Only one species, *M. parvilabius*, is known from the Guyana shield (Luer, 1992).

A. R. Endrés collected material later referred to as *Myoxanthus scandens* near the village of San Ramón, Costa Rica, around 1870. According to the collector's vouchers deposited in W, the same species was also found in the vicinity of the old capital city of Costa Rica, Cartago. Over fifty years later it was collected again by Charles H. Lankester at La Estrella del Guarco, close to Cartago, and this specimen was eventually used by professor Ames to formally describe *Myoxanthus scandens* (as *Pleurothallis scandens*; Ames 1923). According to a manuscript note of the collector on the

holotype sheet, the flowers of this species are “dull raisin purple”.

After studying specimens of this group in the collections of CR, INB, JBL, USJ and W, we noted that the name was apparently applied to two different taxa, one having dark purple flowers and the other yellowish flowers. Further examination revealed additional distinguishing characters between these two taxa, both in vegetative and floral morphology. One of these species was recognized as *Myoxanthus scandens*, while the other is still in need of taxonomical recognition. With the aim of better comparing both entities, we describe and illustrate *M. scandens* as well as the species new to science.

Myoxanthus scandens (Ames) Luer, Selbyana 7(1): 49. 1982. *Pleurothallis scandens* Ames, Sched. Orch. 5: 18-21. 1923. FIG. 1—2.

TYPE. COSTA RICA. Cartago: La Estrella, *C. H. Lankester & A. Sancho 401* A delightful scandent species occurring in forest-ridges. Flowers dull raisin purple (holotype, AMES; isotype, AMES).

Plant epiphytic, caespitose, scandent, up to 60 cm long. *Roots* slender, flexuous, to 1 mm in diameter. *Ramicauls* slender, cylindric, 0.1-0.15 cm in diameter, 0.6-30.0 cm long, enclosed by 3-13 tubular, pubescent sheaths 0.5-4.5 cm long. *Leaves* straight with the ramicaul, coriaceous, elliptic, conduplicate, acute, 2.5-11.0 × 0.5-1.0 cm, narrowly cuneate basally, subpetiolate. *Inflorescence* a fascicle of successive, single flowers, borne at the apex of the ramicaul from a spathe 1 mm long, with flowers usually produced singly, 2-4 mm long including the peduncle 2 mm long. *Floral bracts* tubular, ovate, acute, conduplicate, pubescent, 1 mm long. *Pedicels* 1 mm long, persistent. *Ovary* cylindric, 1.5 mm long. *Flowers* with brown-purple sepals and translucent green petals with longitudinalpurple stripes, the lip purple. *Dorsal sepal* ovate, acute, concave, 4.5 × 2.0 mm, 5-veined. *Lateral sepals* ovate, acute to obtuse, 4.0 × 1.5 mm, 3 to 5-veined, connate for approximately half their length, pubescent at the center of their common surface, the apex erose. *Petals* narrowly ovate, wider at the basal half, contracted into a thickened, apical, serrulate, acute tail, 4.0 mm long, 2.0 mm wide at the basal half. *Lip* oblong, scarcely trilobed, 3.0 mm long, hinged

to the column foot, the lateral lobes near the middle, perpendicular, erect, the disc with a longitudinal pair of parallel lamellae from the lower third to near the apex, the base subtruncate with a pair of small lobules, the apex obtuse, minutely denticulate. *Column* short, stout, semiterete, 2 mm long, provided with an acicular, acuminate tooth on each side of stigma, the clinandrium denticulate, the anther incumbent, the stigma ventral. *Pollinia* two, pyriform, on an elliptic, recurved viscidium.

MATERIAL STUDIED: **Costa Rica. Alajuela:** [San Ramón], La Palma de San Ramón, [1300-1500 m], 29 Agosto 1924, *A. M. Brenes 2291* (CR-34052). [Alajuela: San Ramón], La Palma de San Ramón, [1300-1500 m], 24 octubre 1924, *A. M. Brenes 1536* (CR-26204). **Cartago:** 5.6 km San José side of road leading to Palmital, steep new dirt road up hill from Pan Am highway, 1700–1800 m, epiphytic on exposed tree near edge of forest. Plants to 1 m tall, upright – spreading, flowers extremely dark maroon almost black, 21 Setiembre 1979, *K. S. Walter 79486* (CR). Oreamuno, Cipreses, 9°52'57"N, 83°51'18" W, 1850 m, remnants of primary forest, 23 June 1998, *F. Pupulin et al. 838* (JBL-Spirit). Oreamuno, Cipreses, 9°52'57"N, 83°51'18" W, 1850 m, 23 June 1998, *F. Pupulin et al. 837* (USJ). Turrialba, Torito, [ca. 10°00'00"N, 83°42'00"W, 1500 m], floreció en cultivo en el Jardín Botánico Lankester, 25 enero 2001, *M. Blanco 1820* (USJ). **Heredia:** Heredia, Vara Blanca, en los potreros y partes de bosque secundario pertenecientes al Poás Volcano Lodge cerca del centro de Vara Blanca, 10°10'00" N, 84°10'06" W, 1700 - 1900 m, 03 - 04 agosto 2006, *Karremans 1322 & D. Karremans* (JBL-Spirit) (Fig. 2). **Panama. Panama:** road between El Llano and Cartí, 300 m, 4 Mar. 1976, *C. Luer et al. 1018* (MO, SEL, illustration); Llano-Cartí road, 1 mile past saw mill on dirt road, 300-500 m, 11 Nov. 1979, *C. Todzia et al. 1023* (CR).

ETYMOLOGY: From the Latin *scandens*, “scandent” in allusion to the habit of the plant.

DISTRIBUTION: Costa Rica and Panama.

HABITAT AND ECOLOGY: Epiphytic in lower montane wet and very wet forests, and premontane rain forest at elevations between 1300 and 1900 m in Costa Rica, and epiphytic in premontane wet forests at elevations between 300 and 500 m in Panama. According to

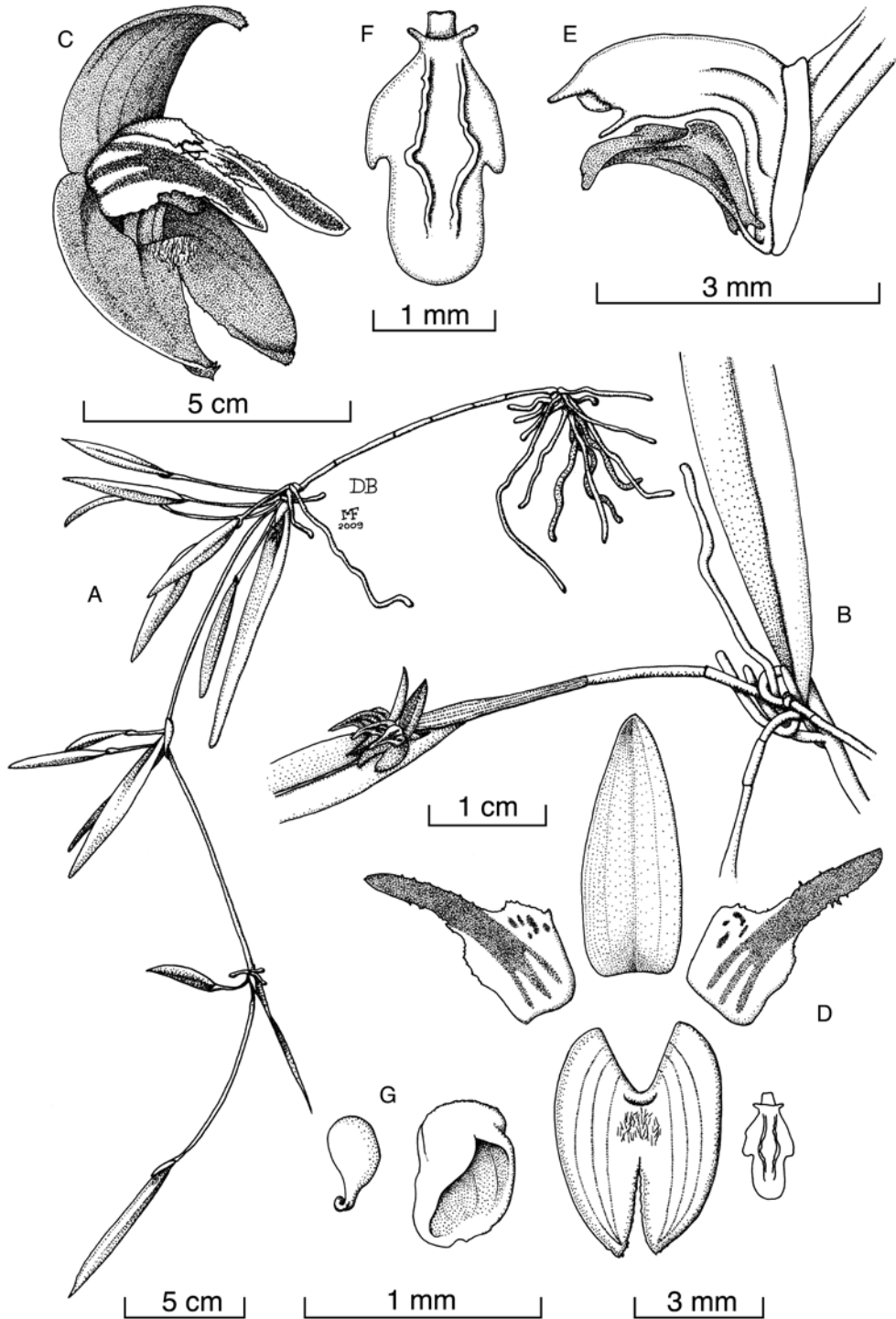


FIGURE 1. *Myoxanthus scandens* (Ames) Luer. A — Habit. B — Detail of the habit. C — Flower. D — Dissected perianth. E — Ovary, column and lip, lateral view. F — Lip, spread. G — Pollinarium and anther cap. Drawn by D. Bogarín and M. Fernández from A. Karremans 1322.

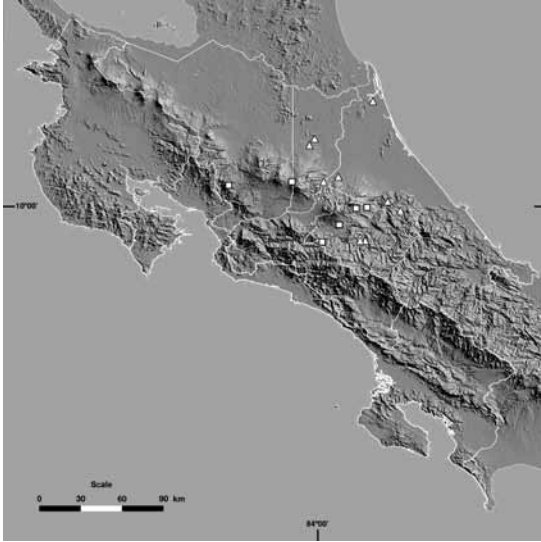


FIGURE 2. Distribution map of *Myoxanthus sotoanum* (Δ) and *Myoxanthus scandens* (\square) in Costa Rica.

data available, this species flowers from December to February.

Myoxanthus scandens is distinguished by the elliptic leaves, dark purple flowers, the purple striped petals, lateral lobes of lip triangular, acute, erect with two keels extending to the apex of the lip, and the long, acuminate processes that flank the stigma.

We are not including here *Pleurothallis pennellia* in the synonymy of *M. scandens*. The species was described in 1976 from Ecuador, on the basis of a specimen flowered in cultivation at the Marie Selby Botanical Gardens (Luer, 1976). Luer (1976) noted the vegetative similarity to *M. scandens*, but described the new species as much less prolific. This, however, may be an artifact due to the juvenile, immature condition of the holotype specimen, and Luer later included it in the synonymy of *M. scandens* (Luer, 1992). The petals of *P. pennellia* are narrowly ovate and shortly obtuse at the apex, while in both *M. scandens* and *M. sotoanum* they are apically contracted into a thickened, acute tail. The lip of *P. pennellia* has two low keels above the middle, while these structures extend from the lower third to the middle of the lip in *M. sotoanum*, and from the base to near the apex in *M. scandens*. Furthermore, the clinandrium of *P. pennellia* is short, leaving the anther partially exposed, while *M. scandens* and *M. sotoanum* have a long, hooded clinandrium, completely covering the anther cap. In our opinion, *P. pennellia* is a

true member of *Myoxanthus*, likely distinct from other species of the genus. It is perhaps co-specific with a Peruvian (or perhaps an Ecuadorian), unvouchered specimen illustrated in Zelenko & Bermúdez (2008). However, we refrain to make the new combination in *Myoxanthus* until we can study more material from the type locality.

Myoxanthus sotoanum Pupulin, Bogarín & M. Fernández *sp. nov.*

TYPE: Costa Rica. Cartago: Jiménez, Pejibaye, La Marta, shore of Río Pejibaye, 9°47'47"N 83°42'55"W, 690 m, epiphytic in secondary vegetation along the river, premontane wet forest, 10 Jan. 2004, *F. Pupulin 5044*, *S. Dalström* & *H. León-Páez* (holotype, CR; isotype, JBL-spirit). Fig. 2—3.

Species *Myoxantho scandenti* (Ames) Luer aemulans, sed foliis linearibus, sepalis brunneis, petalis labelloque flavis, lobis lateralibus labelli obtusis subfalcatis, duobus carinis extensis fere dimidium labelli, dentibus lateralibus columnae acicularis acuminatis praecipue differt.

Plant epiphytic, caespitose, scandent, up to 90 cm long. *Roots* slender, flexuous, to 1 mm in diameter. *Ramicauls* slender, cylindrical, 0.5 cm in diameter, 1-23 cm long, enclosed by 2-6 tubular, pubescent sheaths 0.8-4.0 cm long. *Leaves* straight with the ramicaul, coriaceous, elliptic, conduplicate, acute, 2.5-9.0 x 0.15-0.3 cm, narrowly cuneate, subpetiolate. *Inflorescence* a fascicle of successive, single flowers, borne at the apex of the ramicaul from a spathe 1.0-1.5 x 0.1-0.25 mm, with flowers usually produced singly, 4-6 mm long including the peduncle 2 mm long. *Floral bracts* tubular, ovate, acute, conduplicate, pubescent, 1 mm long. *Pedicels* 2 mm long, persistent. *Ovary* cylindrical, 2 mm long. *Flowers* with brownish-yellowish sepals and yellow petals and lip. *Dorsal sepal* ovate, acute, entire, concave, 5.0 x 2.0-2.5 mm, 3 to 5-veined. *Lateral sepals* ovate, acute to obtuse, entire, concave, 4.5 x 2.0 mm, 2 to 3-veined, connate and pubescent at the center of their common surface. *Petals* ovate, wider at the basal half, gradually contracted into a thickened, apical, serrulate, acute tail, 4-6 mm long, 1-2 mm wide at the basal half. *Lip* oblong, trilobed, 2.5 mm long, hinged to the column foot, the lateral lobes basal, perpendicular to the disc, erect, the disc with a

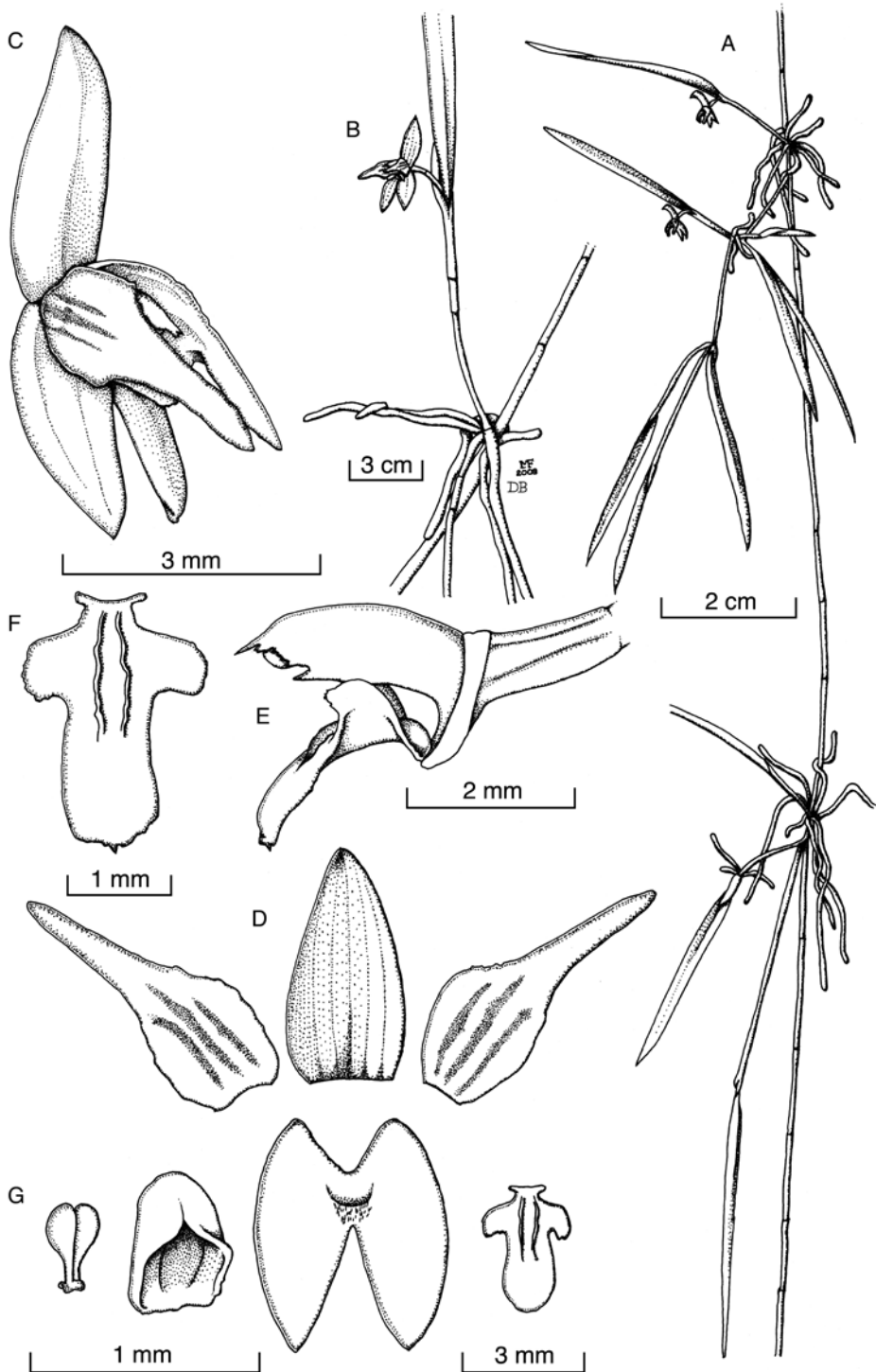


FIGURE 3. *Myoxanthus sotoanum* Pupulin, Bogarín & M. Fernández. A — Habit. B — Detail of the habit. C — Flower. D — Dissected perianth. E — Ovary, column and lip, lateral view. F — Lip, spread. G — Pollinarium and anther cap. Drawn by D. Bogarín and M. Fernández from the holotype.

longitudinal pair of parallel lamellae from the lower third to the middle, the base subtruncate with a pair of small lobules, the apex obtuse, the apex minutely and irregularly erose. *Column* short, stout, semiterete, 2 mm long, provided a triangular, acute tooth on each side of stigma, the clinandrium denticulate with a pair of slender, apical teeth, the anther incumbent, the stigma ventral. *Pollinia* two, pyriform, on a rounded viscidium.

PARATYPES: Costa Rica. **Cartago:** forest on Casa de Tejas Ridge above río Gato, 9°47'N 83°41'W, 800 m, 28 December 1973, *W. Lent 3710* (CR). Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km después de la escuela de Taus, 9°46'51.7"N 83°43'00.4"W, 707 m, 30 abril 2009, *D. Bogarín et al. 6920* (JBL-Spirit). Turrialba, Parque Nacional Barbilla, cuenca del [río] Matina, sendero Principal por río Dantas, 9°58'20.0"N 83°27'10.0" W, 300–400 m, epífita, flor blanca, 11 Noviembre 2000, *G. Mora & E. Rojas 1655* (INB). Turrialba, Parque Nacional Barbilla, cuenca del [río] Matina, sendero Barbilla, hasta la loma, 9°58'20.0"N 83°27'10.0" W, 300–400 m, epífita, flor blanca, 20 Noviembre 2000, *G. Mora & E. Rojas 1722* (INB). **Heredia:** Finca La Selva, OTS Field Station near junction of Puerto Viejo and Sarapiquí rivers, 40–100 m, Camino Circular Lejano 750, 19 marzo 1991, *K. Richardson III* (CR). Finca La Selva, OTS Field Station near junction of Puerto Viejo and Sarapiquí rivers, 40–100 m, Camino Circular Lejano 750, 19 Marzo 1991, *K. Richardson III* (CR). Sarapiquí, La Virgen, Magsasay, banks of Río Peje, 10°24'03.9"N 84°02'53.5"W, 110 m, tropical wet forest, 25 August 2007, *F. Pupulin et al. 6888* (JBL-Spirit). **Limón:** Cerro Coronel, east of Laguna Danto, 10°41'N 83°38'W, 20–170 m, tall evergreen forest on gentle to moderately steep slopes, scandent epiphyte in canopy, flowers white, 15–20 September 1986, *W. D. Stevens 24568* (CR). Siquirres, Siquirres, Guayacán, en potreros bajando el camino frente el bar Guayacán, en las orillas de la Quebrada Quebrador, 10°02'1.44"N 83°32'13.5" W, 477 m, 25 enero 2008, *D. Bogarín 4049 & A. Karremans* (JBL-Spirit). Siquirres, Guayacán, en potreros bajando el camino frente el bar Guayacán, en las orillas de la Quebrada Quebrador, 10°02'1.44"N 83°32'13.5" W, 477 m, 25 enero 2008, *A. Karremans 2311 & D. Bogarín* (JBL-Spirit). Pococí, Cuenca

del [río] Sarapiquí, Guápiles, finca INBio, sendero de Las Aves, 10°11'39.624"N 83°51'39.0980" W, 300–400 m, epífita, flores blanco y morado, 07 Junio 2007, *M. M. Flores et al. 24* (INB). **San José:** [Parque Nacional Braulio Carrillo], sendero "La Botella", 750 m, floreció en cultivo en el Jardín Botánico Lankester, 10 Diciembre 2000, *M. Blanco 1725* (JBL-Spirit, USJ). Sin datos de recolecta, floreció en cultivo en el Jardín Botánico Lankester, 30 setiembre 2009 (JBL-21345-Spirit). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, flowers pale yellow suffused with brown, 18 December 2000, *F. Pupulin 2742* (USJ). Vásquez de Coronado, Parque Nacional Braulio Carrillo, along sendero "La Botella", in primary forest, 10°10'00"N 83°57'20"W, 750 m, epiphytic on liana, sepals translucent white suffused with purple, petals dull white, arching with apices meeting in front of lip, lip yellowish-white, 16 November 1990, *S. Ingram 712 & K. Ferrell* (CR). Vásquez de Coronado, Parque Nacional Braulio Carrillo, along sendero "La Botella", in primary forest, 10°10'00"N 83°57'20"W, 750 m, pale green-yellow suffused with purple spots, 02 January 1991, *S. Ingram 828 & K. Ferrell* (INB).

DISTRIBUTION : Known only from Costa Rica along the Caribbean slopes of the Central Volcanic Cordillera to about 800 m

EPONYMY: Dedicated to the memory of Miguel Angel Soto Arenas (1963-2009), for his outstanding contributions to the knowledge of Neotropical orchids.

HABITAT AND ECOLOGY: Plants have been found epiphytic in tropical wet and very wet forests, premontane rain forest, and premontane wet and very wet forest from near sea level to about 800 m. Flowers between March and September.

Myoxanthus sotoanum is similar to *M. scandens* Ames, from which it differs in the linear leaves (vs. elliptic), brownish-yellowish flowers (vs. dark purple), the yellow petals and lip (vs. purple striped), oblong, obtuse, subfalcate lateral lobes of lip (vs. triangular, acute, erect) with two keels extending nearly to the middle of the lip (vs. extending to the apex of the lip), and the triangular, acute teeth (vs. acicular, acuminate) that flank the stigmatic cavity. It also generally occurs at lower elevations.

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SOME NEW SOBRALIAE FROM COSTA RICA AND PANAMA

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ABSTRACT. A new species of *Elleanthus*: *E. carinatus* and three new species of *Sobralia*: *S. fragilis*, *S. geminata* from Costa Rica and *S. sotoana* from Panama are described and illustrated.

RESUMEN: Una nueva especie de *Elleanthus*: *E. carinatus* y tres nuevas especies de *Sobralia*: *S. fragilis*, *S. geminata* de Costa Rica y *S. sotoana* de Panama se describen y se ilustran.

KEY WORDS/PALABRAS CLAVE: Sobraliae, *Elleanthus carinatus*, *Sobralia fragilis*, *Sobralia geminata*, *Sobralia sotoana*, new species, Costa Rica, Panama.

Here we describe several new species that have been found in the last few years. All are cultivated in the Lankester Botanical Garden, have flowered here, and material has been pressed from the cultivated plants.

Elleanthus carinatus Dressler & Bogarín, *sp. nov.*

TYPE: COSTA RICA. Cartago: límite entre Turrialba y Jiménez, La Suiza, Pejivalle, Fila Rincón de la Esperanza, entre Río Atirro y Río Nubes, 9°46'43.3"N 83°37'36.0"W, 1150 m, bosque muy húmedo premontano, pressed from cult. 10 Aug. 2009, *R.L. Dressler 7069* (holotype: CR; isotype: JBL-spirit). FIG. 1, 8A.

Elleantho cynarocephalo (Rchb.f.) Rchb.f. affinis, bracteis brunneo-incarnatis pallentibus, petalis oblanceolatis, floribus e basi inflorescentiis primis aperientibus differt.

Roots to 8 mm in diameter. *Stems* to 90 cm (doubtless becoming taller); sheaths slightly scurfy. *Leaves* 22-30 x 4-5 cm, petiole ca. 5 mm, blades elliptic-lanceolate, acuminate, with 7 prominent veins beneath. *Inflorescence* capitate, ca. 4.5 x 4.0 cm; lower bracts green, upper bracts pale brownish pink. *Flowers* rose-purple, inflorescence bracts oblong, acute, ca. 2.5 x 7.0-8.0 mm, with prominent median keel distally, this ending in apicule or mucro. *Dorsal sepal* 11 x

3 mm, elliptic, acute. *Lateral sepals* 12.0 x 4.5 mm, symmetrical. *Petals* 10.5 x 3.0 mm, oblanceolate. *Lip* 14-15 x 15 mm, blade flabellate, emarginate, margins serrulate. *Pollinia* 8, obovate.

The genus *Elleanthus* is clearly a relative of *Sobralia*. In the field, larger plants with unbranched stems may be difficult to assign to either genus with confidence unless there are at least remains of an inflorescence.

Garay (1978) recognizes several sections within *Elleanthus*, and treats the members of Section *Cephalelyna*, mostly large or very large plants with capitate inflorescences and a prominent “mentum” beneath the column. For many years, most members of this group were called *Elleanthus capitatus*. Garay (1978) offers a key to the sections of *Elleanthus*, and treats ten distinct species in Section *Cephalelyna*. Now *E. capitatus*, sensu stricto, is a Peruvian species, while the *E. “capitatus”* of Mexico and Central America is *E. cynarocephalus*.

Most, if not all, of the species of this section commonly produce a clear, mucilaginous material on the inflorescence that may serve to protect the flowers and developing buds from insect damage. Neither of the Costa Rican plants that we discuss here produced appreciable mucilage, but flower parts of the new species here described definitely exuded some mucilage when preserved in FAA.

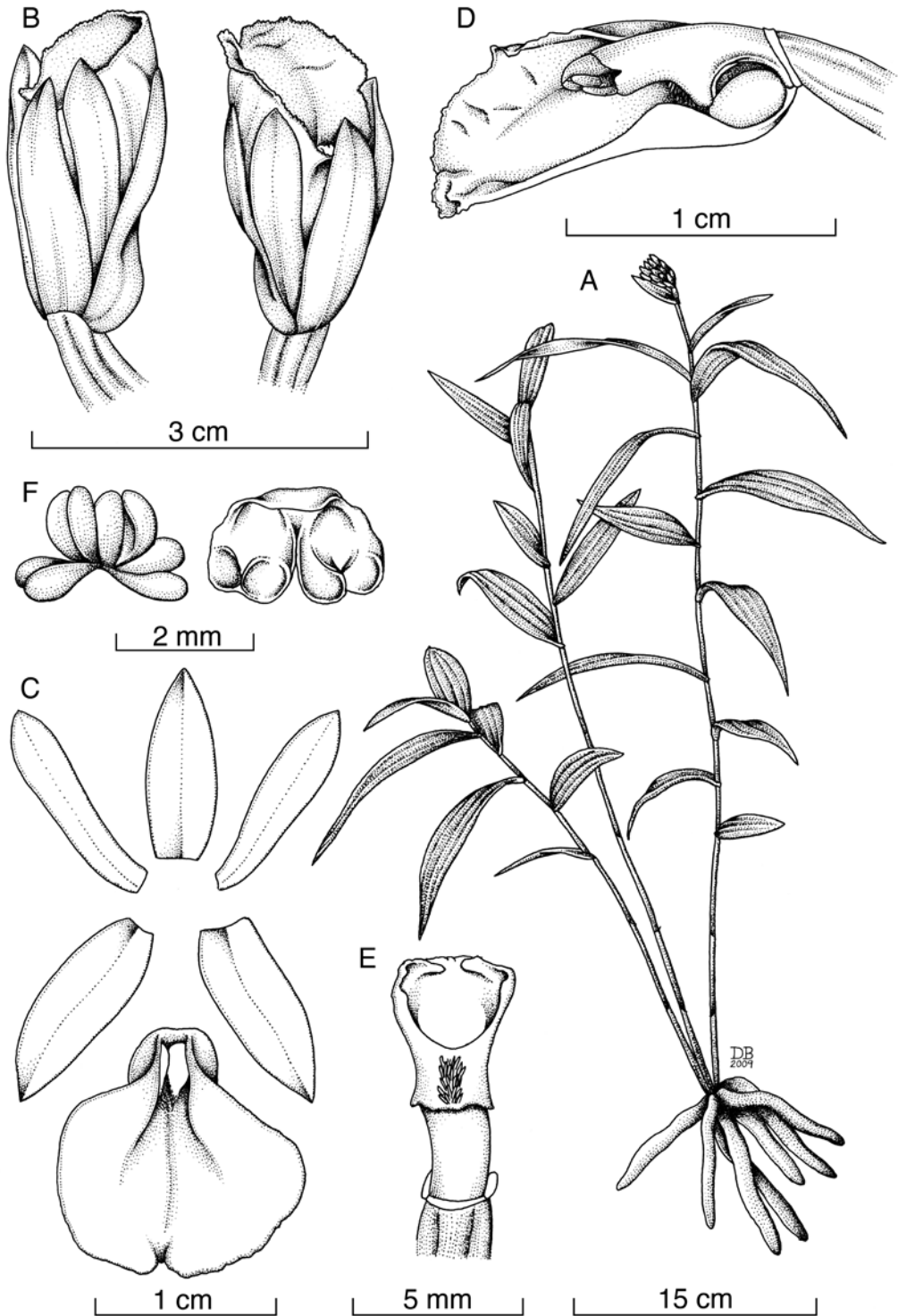


FIGURE 1. *Elleanthus carinatus* Dressler & Bogarín. A — Habit. B — Flowers. C — Dissected perianth. D — Column and lip, lateral view. E — Column, frontal view. F — Pollinarium and anther cap. Drawing by D. Bogarín from the holotype.

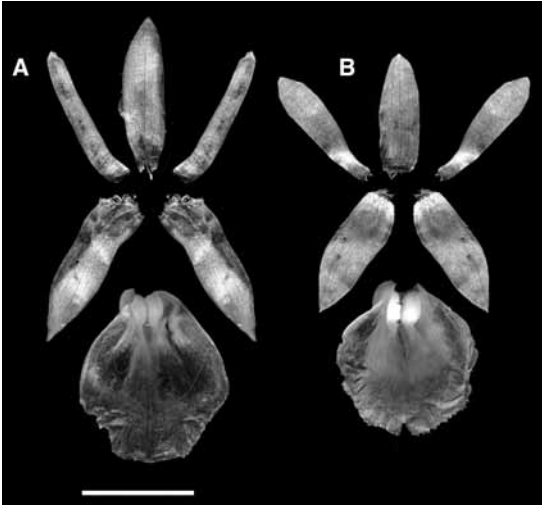


FIGURE 2. Comparison of the dissected perianth of: A — *Elleanthus cynarocephalus* (Dressler 6697). B — *E. carinatus* (Dressler 7069). Scale bar = 1 cm.

Until recently, we believed that there was only one member of Section *Cephalelyna* in Central America, but one of the “Sobralias” collected near Esperanza, in Cartago Province, developed a clearly capitate inflorescence, suggestive of Section *Cephalelyna*. As the inflorescence developed, it was clearly not the same as that of *E. cf. cynarocephalus*¹ that grew near it in the greenhouse. In both plants, the basal bracts of the inflorescence were green, but in *E. cf. cynarocephalus* the upper bracts are rose-purple. In our plant from near Esperanza, the upper bracts may best be described as “pinkish *café con leche*.” Further, the upper bracts are clearly carinate, with each keel ending in an apicule or a mucro. The upper bracts of the *E. cynarocephalus* are without keels, apicule or mucro. The flowers of these two plants are also distinct. In *E. cynarocephalus* the petals are linear or ligulate, as indicated by Garay (“linear-oblong”) for this species (Fig. 2). In *E. carinatus*, the base of the column (basal to the mentum) is much shorter than the rest of the column, while these are subequal in *E. cynarocephalus*; also, the mentum is larger in

¹ We have not seen authentic *E. cynarocephalus* from northern Central America or Mexico. For now, we treat our one species with rose-purple bracts as *E. cf. cynarocephalus*, though it may actually be referable to an unnamed species, or a South American species.



FIGURE 3. Comparison of the column of: A — *Elleanthus cynarocephalus* (Dressler 6697). B — *E. carinatus* (Dressler 7069). Scale bar = 5 mm.

E. carinatus than in *E. cynarocephalus* (Fig. 3). A striking difference in the available material is that the flowers of *E. carinatus* open from the base of the head upwards (Fig. 8A), while those of *E. cynarocephalus* open from the apex downward.

DISTRIBUTION: only known from Costa Rica.

ETYMOLOGY: from the Latin *carinatus*, keeled, referring to the marked keels on the bracts of the inflorescence.

Sobralia fragilis* Dressler & Bogarín, *sp. nov.

TYPE: COSTA RICA. San José: Dota, Falda este del Cerro Nara, 740-840 m, F. Pupulin 1099, D. Castelfranco & L. Spadari, 14 Jan. 1999, flowered in cult., 11 August 2009, *R.L. Dressler 7170* (holotype: CR; isotype: JBL-spirit). FIG. 4, 8B.

Species numerosis (circa 22) carinis farinosis labelli a congeneribus diversa.

Roots 3-6 mm in diameter. *Stems* 75-100 cm, 4-5 mm in diameter basally, 3.5-4 mm distally, dark purplish green mottled with pale green spots, young sheaths similar; leaves broadly elliptic, acute to acuminate, with 7 prominent veins beneath, 15-26.5 × 4-8.6 cm. *Inflorescence* ellipsoid, 3.5-5 × 0.8-1.2 cm, with 2-3 subtending foliar bracts 6-13 × 1.8-5.2 cm. *Ovary* sessile, 1.1-2.2 cm. *Sepals* greenish

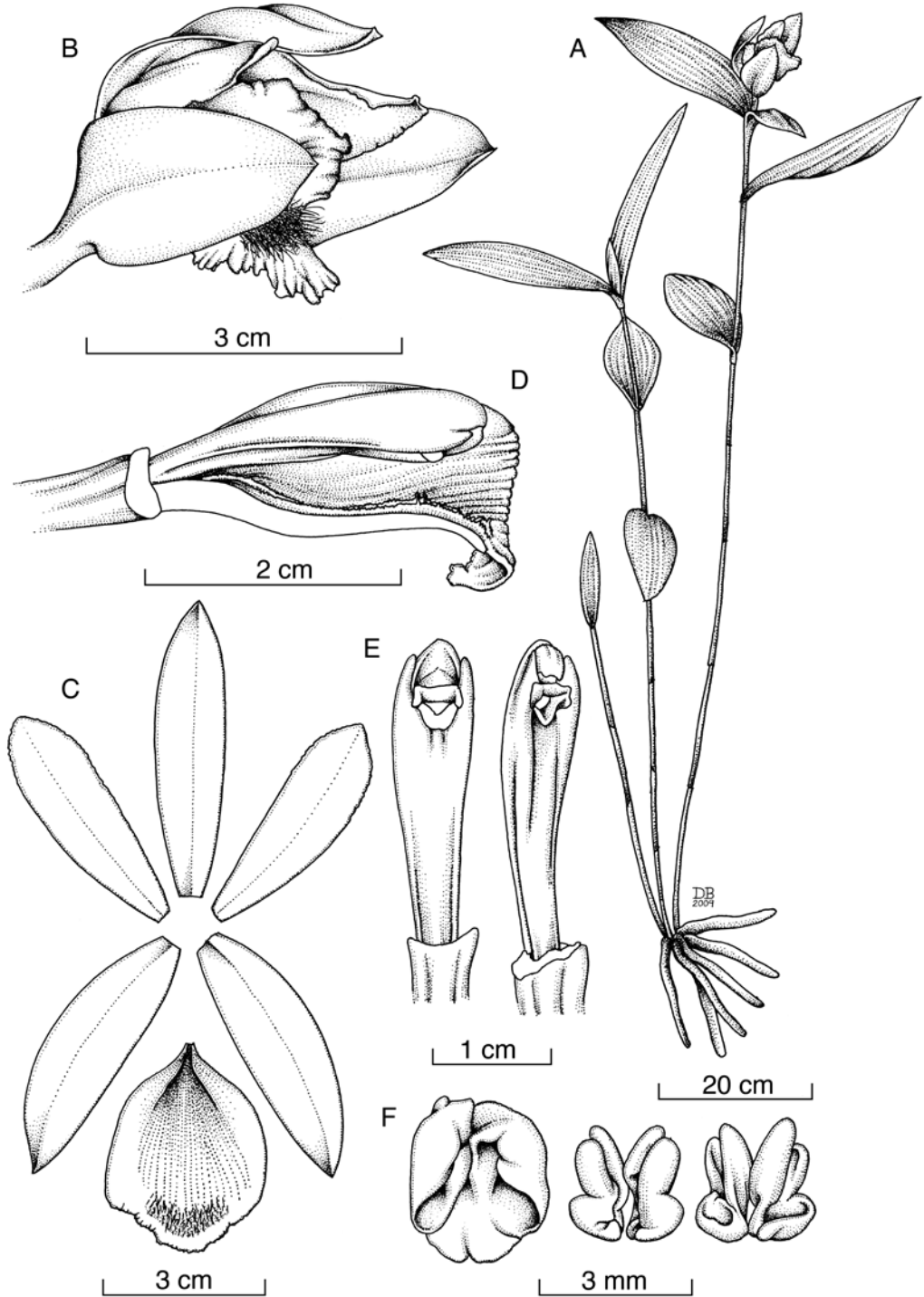


FIGURE 4. *Sobralia fragilis* Dressler & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, frontal and side view. F — Pollinarium and anther cap. Drawing by D. Bogarín from the holotype.

white without, with green apices. *Petals* white or cream with a green median vein without; midlobe of lip yellow. *Lip* with a purplish submarginal band on each side; base of lip minutely striped with white and brown within; sepaline tube 4-8 mm. *Dorsal sepal* elliptic-oblong to oblanceolate, obtuse, apiculate, 3.5-5 x 1.1-1.5 cm. *Lateral sepals* ovate-lanceolate or oblanceolate, obtuse, apiculate. *Petals* narrowly obovate or oblong-elliptic, obtuse, 2.8-4.7 x 1-1.5 cm. *Lip* subquadrate-subobovate, 3.2-4 x 3-3.8 cm, basal calli 7-9 mm; base of lip with ca. 23 low ridges, these becoming higher and more ornate distally. *Column* 20-27 cm x 4.5-6 mm laterally, 5-5.5 cm. dorsoventrally, lateral arms 1-2 mm.

This species is one of the most distinctive known to us. It does not resemble any other species known from Central America. It is, in fact, one of the most difficult to deal with. The base of the lip has about 22 low keels. The keels and the alternating grooves appear as narrow stripes. The keels become much higher in the distal portion of the lip, but they are actually soft and mealy. It is difficult to handle the lip without rubbing off the “keels.” All *Sobralia* flowers are delicate, but it is almost impossible to handle the lips of this species without destroying the surface. Thus, we have chosen the epithet “*fragilis*” for this species. It is quite possible that this species is related to a Colombian species that has been called “*S. suaveolens*.” The so-called “*S. suaveolens*” has prominent “crests” on the lip that are actually a powdery, yellow substance, and may act as pseudopollen to attract female bees that gather the pseudopollen as food for their brood. This Colombian species has the lip very much more deeply divided than either *Sobralia fragilis* or the true *S. suaveolens*. It is quite possible that *S. fragilis* and the misidentified Colombian species are related to each other and they may both attract pollinators by pseudopollen.

We have only two plants of *S. fragilis*, but the species clearly show synchronized flowering, with both plants usually flowering on the same days.

DISTRIBUTION: only known from Costa Rica.

ETYMOLOGY: from the Latin *fragilis*, “fragile”, referring to the delicate, easily damaged surface of the lip.

Sobralia geminata* Dressler & Bogarín, *sp. nov.

TYPE: COSTA RICA. Cartago: Paraíso, Cachi, Peñas Blancas, camino a Cerros Duán, 9°49'51.3"N 83°46'13.1"W, 1400 m, bosque muy húmedo premontano, terrestre cerca del camino, flowered in cult. 1 October 2009, R.L. Dressler 7173 (holotype: CR; isotype: JBL-spirit). FIG. 5, 6, 8C.

A *Sobralia chrysostoma* Dressler similis, floribus minoribus, labello maculis brunneis plerumque aliquantum albo notato recedit.

Roots 5-7 mm in diameter; stems 20-140 cm, basally 5-6 mm in diameter, distally 3.5-5 mm in diameter. *Stems* dark greenish purple mottled with pale green, young sheaths similar, especially opposite the next leaf blade. *Leaves* elliptic or broadly elliptic, acuminate, apiculate, 11-25 x 4-7.4 cm, with 7-9 raised veins beneath. *Inflorescence* ellipsoid, 3.5-4 x 0.7-1 cm; smaller foliar bracts 3-10 x 1.5-5 cm; ovary 10-22 mm, sepaline tube 1-2 cm. *Sepals* greenish cream with green mid-veins, apically green. *Petals* white without, lip yellow with white margins and usually some white on disk, disk with pale brown spots or streaks. *Dorsal sepal* oblong-elliptic or oblanceolate-elliptic, apiculate, 4.2-6.6 x 1.25-1.8 cm. *Lateral sepals* oblong-elliptic or narrowly obovate, acute, 4.5-6 x 1.5-2.3 cm. *Petals* oblong-elliptic or narrowly obovate, subobtusate to subacute; 4.3-7.1 x 1.6-2.5 cm. *Lip* obovate, 5.3-6.5 x 4.2-4.8 cm, basal calli 0.8-1.8 cm, median keels 4-9, low, sometimes with 1-2 shallow grooves, midlobe crisped. *Column* 2.8-4 cm x 5-9 mm laterally x 5-8 mm dorsoventrally; lateral lobes (arms) small, tooth-like, 1.5-1.6 mm.

PARATYPES: Costa Rica. **Alajuela:** San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10°08'58.7"N 84°34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, R.L. Dressler 7011, A. Karremans & F. Pupilin, 19 February 2008, flowered and pressed in cult. in Lankester Botanical Garden, July 2009, R.L. Dressler 7172 (CR). **Cartago:** Jiménez, Pejibaye, Alto del Humo, 23 May 2005, R.L. Dressler 6561, flowered and pressed in cult. in Lankester Botanical Garden, 14 August 2007, R.L. Dressler 6947 (CR). Paraíso, Orosi,

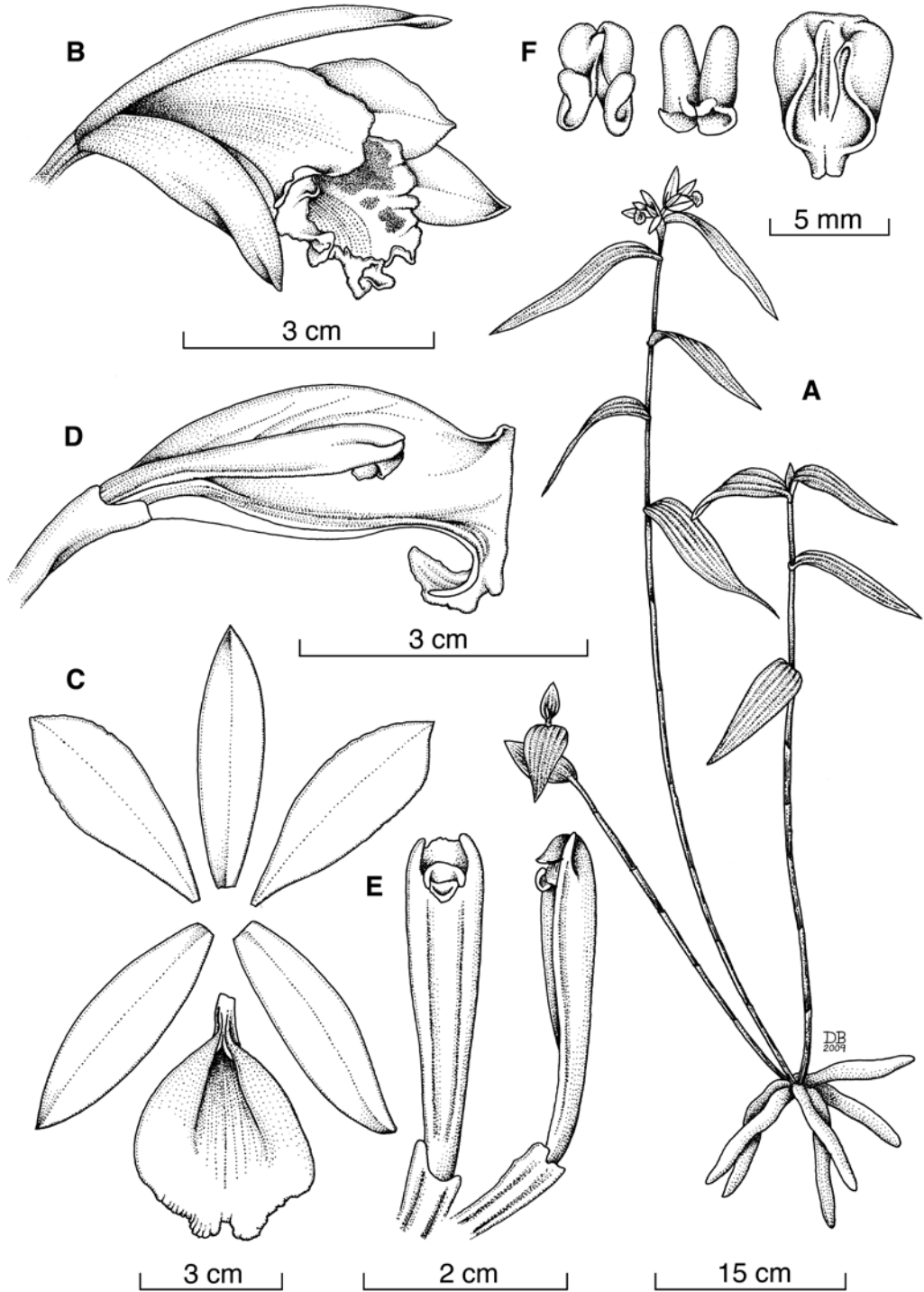


FIGURE 5. *Sobralia geminata* Dressler & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, lateral view. E — Column, frontal and side view. F — Pollinarium and anther cap. Drawing by D. Bogarín from the holotype.

Tapantí, road between Tapantí and Tausito, ca. 500 m before Tejos restaurant, 9°46'16.5"N 83°47'24.6"W, 1453 m, premontane wet forest, *R. Dressler 6661*, *M.A. Blanco & D. Bogarin*, 23 December 2005, flowered and pressed in cult. in Lankester Botanical Garden, 6 July 2006, *R.L. Dressler 6788* (CR). Turrialba, La Suiza, road between Pacayitas and La Suiza, 2 km south of Pacayitas, 9°52'29.9"N 83°35'03.6.4"W, 1150 m, premontane wet forest, 8 March 2006, *R.L. Dressler 6673*, *D. Bogarin*, *A. Karremans & F. Pupulin*, flowered and pressed in cult. in Lankester Botanical Garden, 10 July 2006, *R.L. Dressler 6789* (CR).

DISTRIBUTION: only known from Costa Rica.

ETYMOLOGY: from the Latin *geminatus*, "twinned," referring to the usually paired flowers.

We first found small plants of this species in 2005. When they flowered, the flowers reminded us of *S. chrysostoma*, but we found the flowers to be consistently different from those of *S. chrysostoma*, so we thought it to be an unnamed species. In May of 2007 one of us (RLD) travelled to the northeast of Cartago Province, hoping to find a new species once found near Bonilla Arriba. There were colonies of a *Sobralia* along the roadsides and most of the youngest mature stems each had 2 capsules. My first thought was "The pollinators must be very efficient here," but it was later clear that this population (Pacayas-Santa Cruz), at least, is self-pollinating. This was confirmed when other plants in the Lankester Botanical Garden often set fruits without pollination. Most of the plants produce only two flowers on each stem (either simultaneously or serially), so we have called it *Sobralia "geminata"*, because of the "twin" flowers. As one might expect from a partially self-pollinating species, there is local variation. Obviously, where the flowers are consistently selfed, bees do not carry mutant genes from one colony to another. In San Ramon, we found an attractive form that had the median groove on the lip a bit wider and sometimes had a slender, jointed, column appendage (in *Sobralia*, this appendage is more an "arm," than a "wing"). This was so different from anything else we had seen in *Sobralia* that we thought it to be a new species. However, when the same plants flowered

again, they usually lacked the unique appendage, and they were self-pollinating.

The flowers of *Sobralia geminata* resemble those of *S. chrysostoma*, but they are consistently smaller, and they also have brownish spots or streaks on the lip, and some white near the apex. *Sobralia chrysostoma* frequently has dark purplish spots on the stems and sheaths, while the stems of *S. geminata* are consistently more heavily spotted than any other species in our area. The form of the stigma is quite variable in this species. The stigma varies a good deal in size, often being cuplike, as in most other species, or it may be straight, tongue-like, and subparallel with the column axis. In this latter pattern, the pollen probably germinates on the upper side of the stigma, thus accomplishing self-pollination.

Most *Sobralia* species are markedly synchronized (or "gregarious") in their flowering, often flowering on the same day over a large area. One would not really expect a self-pollinating population to follow strict synchrony, yet the plants of this species in Lankester Botanical Garden usually flower on the same days. The plants collected south of Cartago have consistently flowered on the same days, even though they are quite self-pollinating. One doubts that there is much selective pressure for synchrony in self-pollinating plants, but, at the same time, there is probably little selective pressure against synchrony in such populations.

Our first impression of *S. geminata* was that it was predominantly self-pollinating. We have seen some selfing in most of the plants we have cultivated, as this description was in preparation, we had a number of plants flowering on 31 August 2009 and again on 9 September. Of the 16 flowers produced on 31 August, there were 6 capsules; while on 9 September there were 24 flowers, of which 15 remained as capsules. It is clear that the populations of Pacaya - Santa Cruz and Cartago - Cangreja are largely self-pollinating. One of the large plants from Cartago - Cangreja, however, had flowered heavily about 6 months earlier, and 3 capsules were allowed to remain on the plant. This plant has not produced any flowers in the recent flowerings. The two large plants from Cachi have flowered along with the rest of the *S. geminata*, but no capsules developed on either of these plants. Similarly, Ademar Silveira reports *S. geminata* in the buffer zone northeast of the

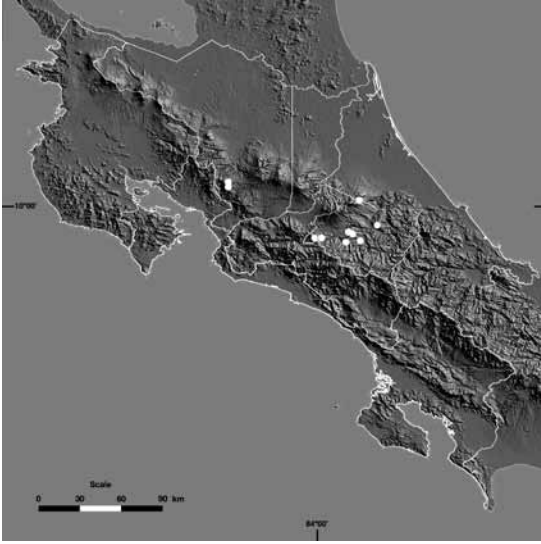


FIGURE 6. Distribution map of *Sobralia geminata* in Costa Rica.

Tapanti Refuge, but has observed no self-pollinating in the species in that area.

Now that we know *S. geminata*, we find plants of this species nearly everywhere we go in central Costa Rica. Indeed, we are rather tired of seeing them.

***Sobralia sotoana* Dressler & Bogarín, sp. nov.**

TYPE: PANAMA. Veraguas, collected near road north of Santa Fé de Veraguas, flowered in culture in Jardín Botánico Lankester, pressed from cultivation, 8 August 2009, R.L. Dressler 7168 (holotype: CR; isotype: JBL-spirit). FIG. 7, 8D.

Species *Sobralia aspera* Dressler & Pupulin similis, labello interius intense aurantiaco, callis basalibus farinosis differt.

Roots to 5 cm in diameter. *Stems* 33-75 cm, ca. 3 mm in diameter basally, 2 mm distally, sheaths slightly scurfy. *Leaves* elliptic or lance-elliptic, long acuminate, 15.0-23.5 x 2.2-5 cm. *Inflorescence* 3-5.0 x 0.5 cm, outer bract acuminate, inflorescence usually horizontal or nodding; subtending foliar bracts acuminate, 15-16 x 1.4-1.7 cm. *Ovary* sessile, 13-17 mm. *Sepaline tube* 12-15 mm. *Dorsal sepal* 3.3-4.5 x 1-1.6 cm, elliptic or lanceolate, subobtuse. *Lateral sepals* elliptic-lanceolate, tapering, 3.2-4.5 x 1.1-1.5 cm. *Petals* obovate, subobtuse, 3.1-3.5 x 1.2-1.3 cm.

Lip oblong-obovate, 4-4.2x 2.8-3.1 cm, without keels; basal calli ca. 6 mm; column clavate, markedly thicker below stigma, 23-24 cm x 0.5 mm laterally x 4-4.5 mm dorsoventrally.

DISTRIBUTION: only known from Panama.

EPONYMY: In honor of Miguel Angel Soto Arenas, to whom this issue of Lankesteriana is dedicated.

When we visited Finca Dracula (Cerro Punta, Panama) in 2006, there were two relatively small *Sobralias* flowering. The staff at Finca Dracula referred to one as “Veraguas” and the other “Santa Fe,” but the city of Santa Fe is in Veraguas province, so these terms seemed a bit unclear. Erick Olmos explained that both species were found in the same area, near a lake north of Santa Fe, on the road that may eventually reach Calovébora, on the Caribbean coast. In any case, “Veraguas” proved to be indistinguishable from *Sobralia aspera*, earlier described from Costa Rica (Dressler & Pupulin 2008), while the other is clearly a distinct species. Further, the Costa Rican and the Panamanian plants of *S. aspera* flower on the same days, thus supporting their specific identity. Both of these resemble *Sobralia leucoxantha*, *S. macra*, *S. kruskayae* and *S. tricolor*, while *Sobralia* “Santa Fe” is clearly distinct from the other species just mentioned. The plant had produced very few flowers in the first year in Costa Rica, but in 2009 it has been quite floriferous.

Sobralia sotoana resembles *S. aspera* vegetatively, though the plant is a bit smaller. The upper stems are weakly but distinctly zig-zag, and the inflorescences much more markedly nodding, or reflexed, so the flowers are somewhat pendant. The flowers are a bit smaller and the lips are intense orange within with a narrow white margin.

ACKNOWLEDGEMENTS. We acknowledge the scientific services of the Costa Rican Ministry of Environment, Energy and Telecommunications (MINAET) and its National System of Conservation Areas (SINAC) together with Autoridad Nacional del Ambiente (ANAM) of Panama, for issuing the collecting permits under which wild species treated in this paper were collected, and for extending the necessary documentation to import orchid specimens from abroad for comparison. We are indebted to Andrés

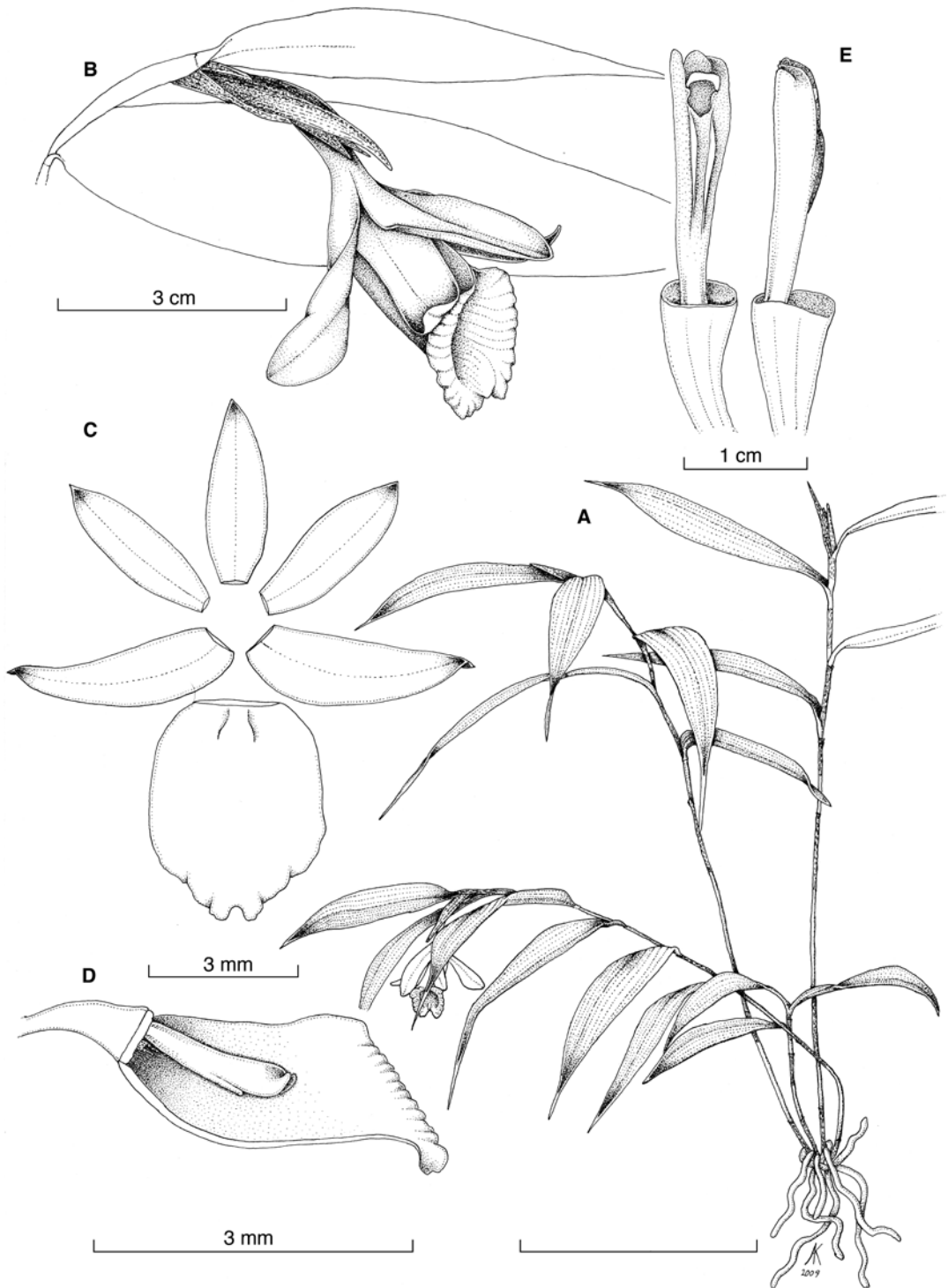


FIGURE 7. *Sobralia sotoana* Dressler & Bogarín. A — Habit. B — Flower. C — Dissected perianth. D — Column and lip, side view. E — Column, frontal and side views. Drawing by A. Karremans from the holotype.

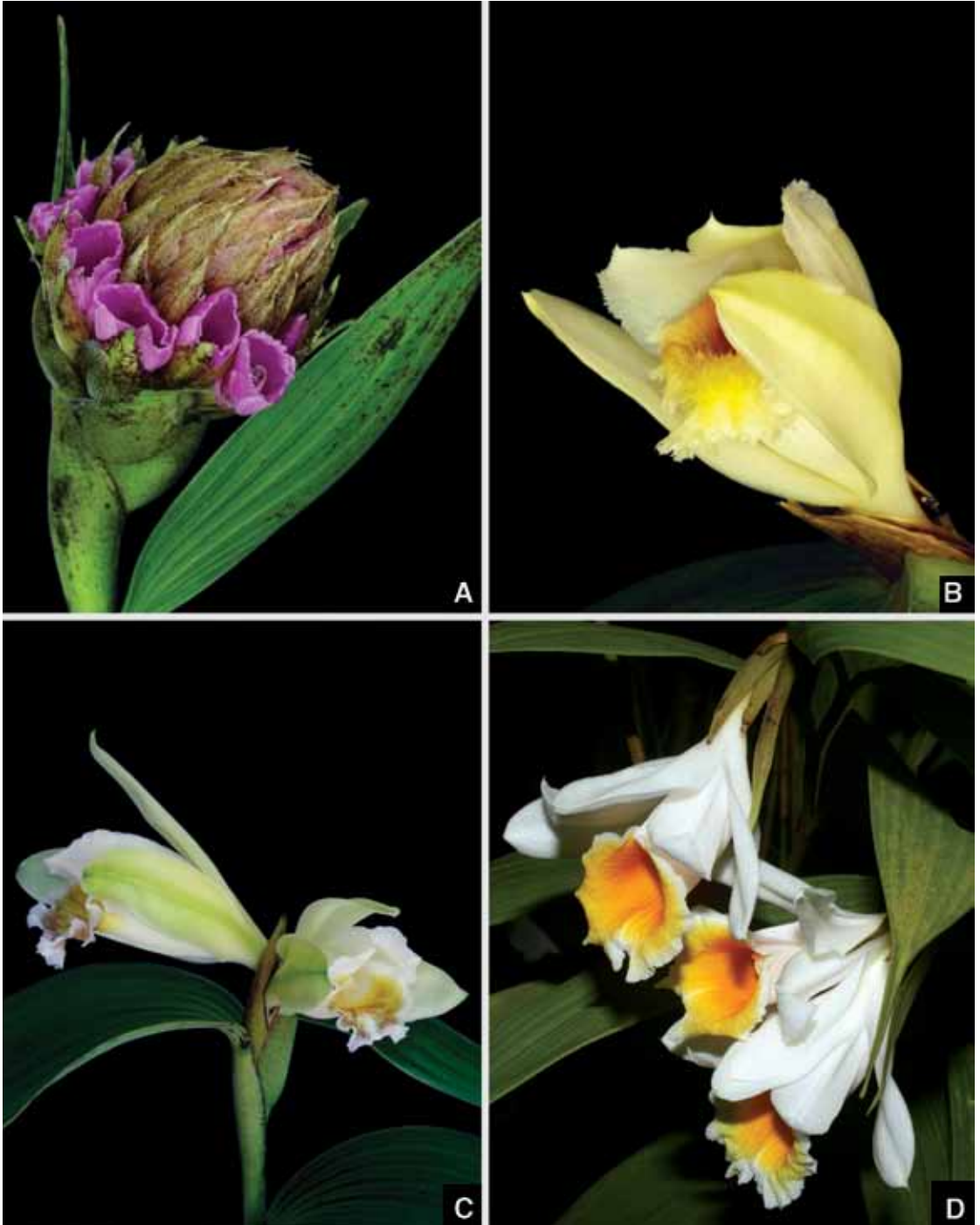


FIGURE 8. Flower morphology of: A — *Elleanthus carinatus*. B — *Sobralia fragilis*. C — *Sobralia geminata*. D — *Sobralia sotoana*. All pictures taken from the clonotypes. A — C by D. Bogarin, D by K. Dressler.

Maduro and Erick Olmos of Finca Dracula, Panama, who provided critical material and information to describe this species. Adam Karremans kindly prepared the drawing of *S. sotoana*. This article is part of Project 814-A7-196, “Systematic studies of *Sobralia*,” supported by the Vice-Presidency of Research, University of Costa Rica.

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LANKESTERIANA

***LEPANTHES ARENASIANA* (PLEUROTHALLIDINAE: ORCHIDACEAE), A NEW SPECIES FROM COSTA RICA**

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ABSTRACT. *Lepanthes arenasiana* from the Talamanca range in Costa Rica is described and illustrated. It is most similar to *L. lancifolia* but differs in having denticulate sepals, the petals with the upper lobe oblong, narrowing at apex and terminating as a short apicule, and the lower lobe basally ovate and straight, filiform towards the apex.

RESUMEN: Se describe e ilustra *Lepanthes arenasiana* de la Cordillera de Talamanca en Costa Rica. Es similar a *L. lancifolia* pero difiere en los sépalos denticulados, los pétalos con el lóbulo superior oblongo, estrechándose hacia el ápice y terminando en un corto apículo, y el lóbulo basal ovado, recto y filiforme hacia el ápice.

KEY WORDS/PALABRAS CLAVE: Orchidaceae, Pleurothallidinae, *Lepanthes arenasiana*, new species, Costa Rica, taxonomy

With 112 species currently recognized, *Lepanthes* is one of the most diverse genera of the Pleurothallidinae in Costa Rica. After Luer (1996), the genus has not been treated formally by botanists for the flora of Costa Rica, however during the past 10 years, studies on *Lepanthes* yielded 13 new species and two new records (Pupulin 2001, Blanco 2003, Pupulin & Bogarín 2004; Pupulin *et al.*, 2009). It is worth noting that 80% of the species registered are endemic (Ossenbach *et al.* 2007, Pupulin *et al.* 2009). Because of the narrow geographic distribution of most of the species, the number of undescribed species increases when specimens are gathered in little explored areas. As an example, three new species were recorded from a single field trip in the Queverí region of Tapantí National Park, a rich plant species area but poorly sampled botanically (Pupulin *et al.* 2009).

The awareness of the great diversity concerning *Lepanthes* has increased through the systematic field trips carried out by the researchers of Lankester Botanical Garden. As a result of two ongoing projects: Inventory and taxonomy of Neotropical Orchidaceae and Systematic studies on the Pleurothallidinae of Costa Rica, it has been possible to survey unexplored areas of the country. Another *Lepanthes* from the

vicinities of Queverí, in the Talamanca mountain range is described here:

Lepanthes arenasiana Bogarín & M. Fernández, *sp. nov.*

TYPE: Costa Rica. Cartago: Cartago, San Francisco, Muñeco, 5.6 km south of Muñeco, between Alto Belén and Alto Cedral, 9°44'54.5"N 83°53'21.7"W, 2112 m, lower montane rain forest, epiphytic in secondary forest, 27 may 2009, *D. Bogarín 6624, R. Gómez, Y. Kisel & R. Trejos* (holotype: JBL; isotypes: CR, USJ). FIG. 1

Species habitu cum *Lepanthes lancifolia* Schltr. optime congruens, sed sepalis ciliatis, acutis, lobo superno petalorum oblongo apice decrescenti in breve apiculum, lobo infero in base ovato deinde usque ad apicem filiformi differt.

Epiphytic, caespitose, pendent *herb*, up to 10 cm long. *Roots* slender, flexuous, to 1 mm in diameter. *Ramicauls* slender, pendent, 4.0—10.5 cm long, enclosed by 7–12 glabrous, lepanthiform sheaths, the ostia minutely ciliate, ovate, acuminate and slightly dilated. *Leaves* subcoriaceous, narrowly ovate, conduplicate, acuminate, emarginate, with a short apiculus, 1.0—4.0 x 0.7—1.1 cm, the rounded

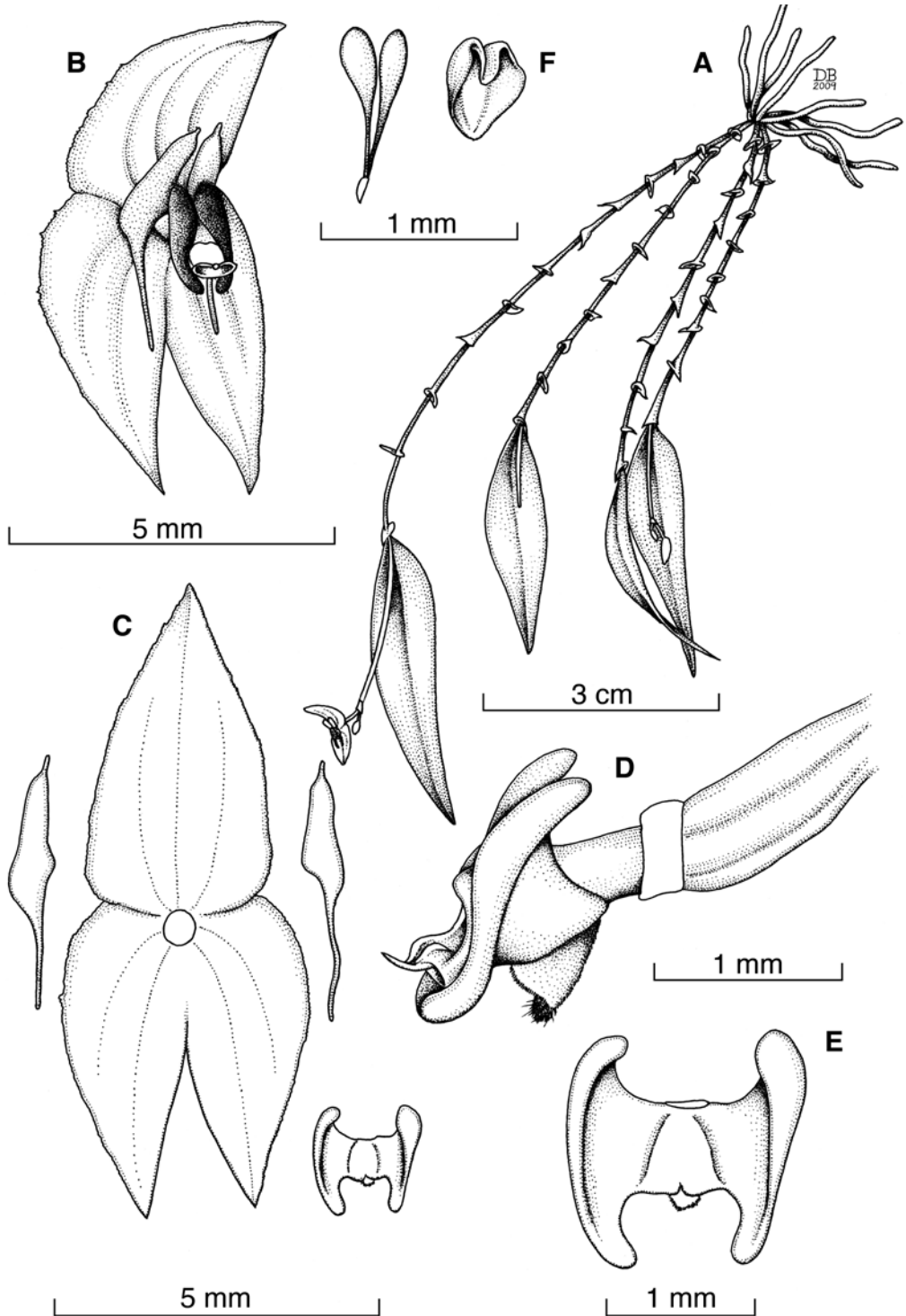


FIGURE 1. *Lepanthes arenasiana* Bogarín & M. Fernández. A — Habit. B — Flower. C — Dissected perianth. D — Lip and column, lateral view. E — Lip, frontal view. F — Pollinarium and anther cap. Drawing by D. Bogarín from the holotype.

base narrowing into a petiole less than 1 mm long. *Inflorescence* racemose, distichous, glabrous, successively flowered, borne above the leaf, shorter than leaves, up to 3 cm long, peduncle 2.2 cm long, rachis 7 mm long. *Floral bracts* ovate, acuminate, conduplicate, membranaceous, 2 mm long, glabrous. *Pedicels* 2 mm long, persistent. *Ovary* to 1 mm long, provided with trichomes along the keels of the carpel divisions. *Flowers* with the sepals yellowish, the petals bright yellow, the lip scarlet red, the column white. *Dorsal sepal* ovate to oblong, acute, denticulate, slightly concave, dorsally with three ciliate keels, connate to the lateral sepals for about 1.2 mm, 5.0 x 2.5 mm. *Lateral sepals* narrowly ovate, acute, denticulate, dorsally with three ciliate keels, connate for 1.2 mm, 2.3 x 5.0 mm. *Petals* transversely bilobed, ciliolate, 1 x 4 mm, the upper lobe oblong, narrowing at apex and terminating as a short apicule, the lower lobe basally ovate, filiform towards the apex. *Lip* bilobate, adnate to the column, the blades oblong with rounded ciliolate ends and falcate apex, embracing the column 1.3 x 2.0 mm, the connectives terete, oblong to 6 mm long, the body thick, oblong, connate to the base of the column, the appendix thick, oblong, pubescent, apically with a minute pubescent apicule. *Column* cylindrical, 1.2 mm long, mucronate, the anther and stigma ventral. *Pollinia* two, ovoid, basally filiform. *Anther cap*, triangular, cucullate.

DISTRIBUTION: only known from the northwestern part of the Caribbean watershed of the Talamanca mountain range in Costa Rica, in the drainage of Río Macho, southern of Cartago Province.

HABITAT AND ECOLOGY. The only known population was found growing epiphytically in lower montane rain forest, in secondary vegetation, on twigs and branches covered by mosses in shady condition, at 2100 m elevation.

Eponymy: The specific epithet honors Miguel Ángel Soto Arenas, a Mexican orchidologist who did great contributions to the knowledge of the family in the Neotropics.

In Costa Rica, *L. arenasiana* resembles the habit of *L. clarae* Luer & J. Hermans, *L. demissa* Luer, *L. lancifolia* Schltr., *L. machogaffensis* Pupulin & D.

Jiménez and *L. tridens* Ames, all having plants 5-15 cm long and narrowly elliptic-ovate, acuminate leaves (Luer 2003). The flowers are most similar to those of *L. lancifolia* (Schlechter 1923) but differ in the denticulate sepals (vs. entire), the petals with the upper lobe oblong (vs. obovate), narrowing at apex and terminating into a short apicule (vs. obtuse), and the lower lobe basally ovate and straight, filiform towards the apex (vs. oblong, obtuse, subfalcate).

ACKNOWLEDGEMENTS. The scientific services of Ministerio del Ambiente, Energía y Telecomunicaciones de Costa Rica (MINAET) and Sistema Nacional de Áreas de Conservación (SINAC) for issuing the Scientific Passport N. 1281 under which wild species treated in this study were collected. The present paper is part of the Project 814-A7-015, "Inventario y taxonomía de la flora epífita de la región Neotropical — Orchidaceae", sponsored by the Vice-Presidency of Research, University of Costa Rica.

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LANKESTERIANA

SOTOA, A NEW GENUS OF SPIRANTHINAE (ORCHIDACEAE) FROM MEXICO AND THE SOUTHERN UNITED STATES

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ABSTRACT. Generic placement of “*Deiregyne*” *confusa* and “*D.*” *durangensis* has been inconsistent among several recent classifications of subtribe Spiranthinae based mainly on floral characters. In this work, we assessed the systematic position of these two species by means of cladistic parsimony analyses of nuclear (nrITS) and plastid (*trnL-trnF*) DNA sequences of 36 species/21 genera of Spiranthinae. Additionally, perceived differences in habitat preference between the two species were evaluated using geographic information system and niche modeling tools. Our results show that, in spite of their striking similarity in overall flower morphology, “*D.*” *confusa* and “*D.*” *durangensis* are only distantly related to one another. Instead, the former species is strongly supported as sister to *Svenkoeltzia*, whereas the latter groups with *Schiedeella*. Niche modeling revealed noticeable differences in the two species’ ecological preferences; no overlap of their potential distribution areas (as inferred using the Maxent modeling method) was predicted. A new monotypic genus, *Sotoa*, is proposed to accommodate “*Deiregyne*” *confusa* on the basis of genetic, morphological and (inferred) reproductive differences from other genera of the subtribe. The main morphological feature distinguishing *Sotoa* from other Spiranthinae is the folding of the bottom surface of the nectary, which is deeply concave from outside, resulting in an internally convex surface that is covered by dense pubescence.

KEY WORDS: Molecular phylogenetics, niche modeling, Orchidaceae, *Sotoa*, Spiranthinae.

In the early 1980s, Harvard orchidologist Leslie A. Garay described *Deiregyne confusa* Garay as a new species of Spiranthinae from Mexico and the southern United States. According to Garay (1982), all the specimens he assigned to *D. confusa* had previously been misidentified as *Spiranthes durangensis* Ames & C.Schweinf. (= *Deiregyne durangensis* [Ames & C.Schweinf.] Garay). Garay distinguished *D. confusa* from *D. durangensis* by its glandular-pubescent sepals, a differently proportioned labellum with a different callus at its base, and the shape of the rostellum [remnant] (Fig. 1). Balogh (1982; also as Burns-Balogh 1986) placed *D. durangensis* in *Schiedeella* Schltr., as did Schlechter (1920) previously with its synonym, *Schiedeella saltensis* (Ames) Schltr. (based on the illegitimate *Spiranthes saltensis* Ames, non Grisebach 1879). Subsequently Szlachetko (1991, 1993) included both *D. confusa* and *D. durangensis* in his newly created section

Lueretta Szlach. within the genus *Funkiella* Schltr. He treated *D. confusa* as a subspecies of *Funkiella durangensis* (Ames & C.Schweinf.) Szlach. because the distinguishing features noted by Garay (1982) vary substantially. More recently, however, Szlachetko *et al.* (2005) raised *Funkiella durangensis* subsp. *confusa* (Garay) Szlach. to species rank, as *Funkiella confusa* (Garay) Szlach., Rutk. & Mytnik, without a discussion of their rationale.

In the course of phylogenetic studies within subtribe Spiranthinae and other research focused on Mexican orchid diversity, the authors have had the opportunity to examine a number of specimens of both *D. confusa* and *D. durangensis*. Superficially plants and flowers of both species look very alike, which may explain the long-standing confusion reported by Garay (1982). However, under closer scrutiny, noticeable differences in floral indumentum and in the morphology of the

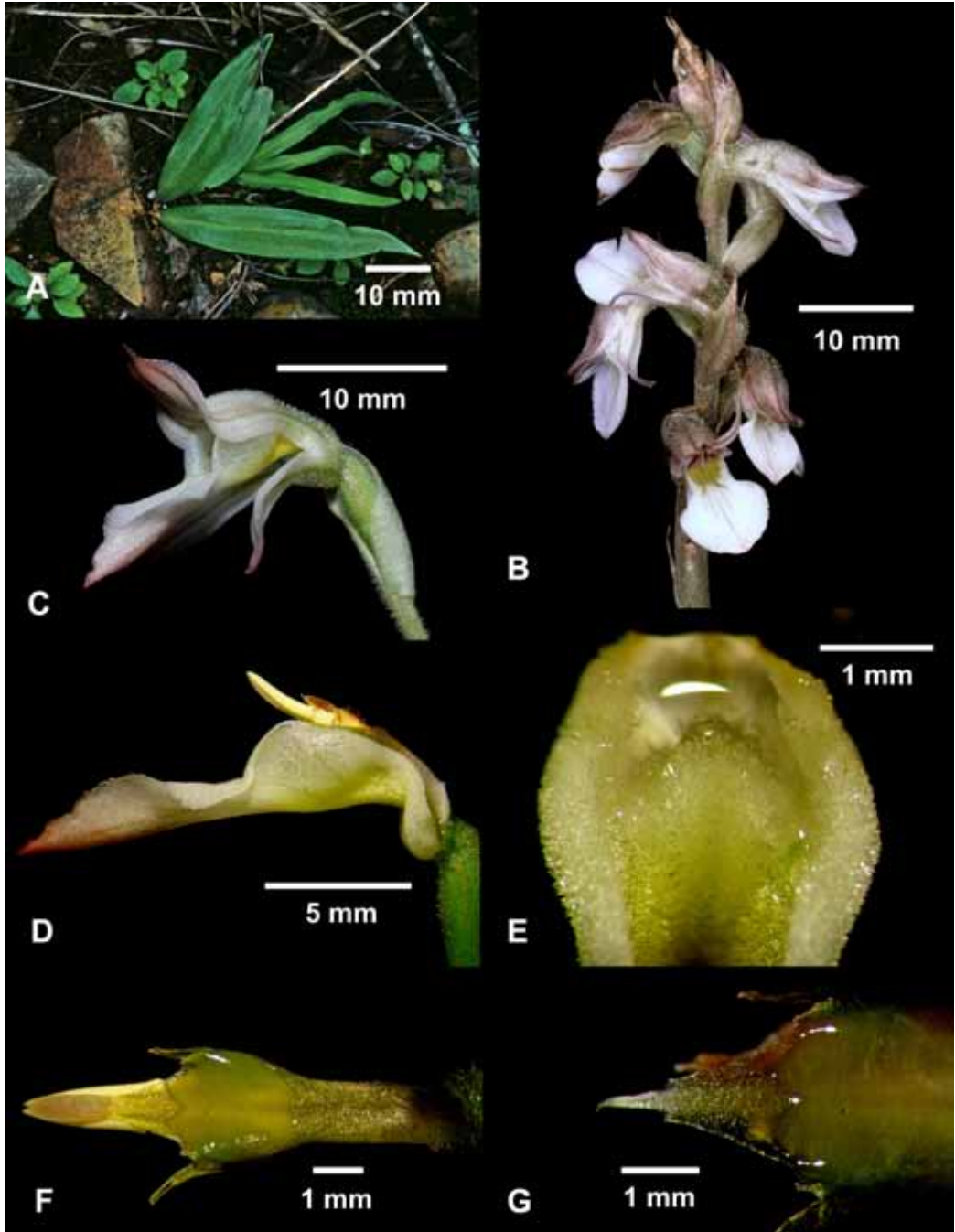


FIGURE 1. Morphology of *Sotoa confusa*. A. Plant *in situ* in Oaxaca during the season of vegetative growth, showing three oblong leaves forming a rosette. B. Inflorescence of a plant from Oaxaca (*Salazar 6575*). C-F. Flower and floral details of a plant from Guanajuato (*Reyes 6885-bis*). C. Flower from the side. D. Labellum and column from the side, with the other perianth segments excised. E. Inside of the nectary, showing the pubescent convexity and some nectar toward the base above it. F. Column with pollinarium in place, from below. G. Column apex after removal of the pollinarium, from below. Photo by G. A. Salazar.

nectary are evident. In *D. durangensis* the ovary bears a dense covering of opaque, curly, intermingling septate trichomes appressed against its surface; such trichomes barely reach the bases of the sepals and most of their outer surface is glabrous (or more precisely, cellular-papillose). In contrast, in *D. confusa* both the ovary and the proximal one half of the outer surface of the sepals bear translucent, sparse erect trichomes (instead of appressed) with a distinct apical swelling, hence the glandular pubescence described by Garay (1982). At the same time, in *D. durangensis* the bottom surface of the nectary at the base of the labellum is flat but bears a fleshy, lunate callus covered by short papillae, whereas in *D. confusa* the bottom of the nectary lacks a distinct callus. Instead, the bottom surface of the nectary is deeply concave from outside, resulting in an internally convex surface covered by dense pubescence (Fig. 1D). In rehydrated flowers from pressed specimens, the internal convexity of the nectary of *D. confusa* often looks like a longitudinal pubescent ridge. Therefore, the aforementioned characters allow for the distinction of the two species, as stated previously by Garay (1982), although the other features mentioned by him, namely lip shape and proportions, and rostellum remnant structure, seem to vary within each species and do not appear to provide clear-cut distinguishing attributes.

Besides their structural dissimilarities, there seem to be differences as well in their geographical ranges and ecological preferences. *Deiregyne durangensis* has a relatively restricted distribution, being known from the surroundings of the town of El Salto, state of Durango, in the Sierra Madre Occidental (including the type locality), plus a few of additional locations in the Estado de México (Luer 1975) and Michoacán (McVaugh 1985). On the other hand, *D. confusa* is a widespread species in eastern Mexico, barely reaching Texas (USA) and spreading through the Chihuahuan Desert to south of the Mexican Plateau, in the states of Coahuila, Estado de México, Guanajuato, Hidalgo, Jalisco, Nuevo León, Puebla, Oaxaca, San Luis Potosí, and the Distrito Federal (Salazar 2009; Salazar *et al.* 2006; Peinado & Riojas 2008) (Fig. 2A). As for their habitat preferences, *D. durangensis* inhabits in grassy open areas in pine-oak forest, and at least some of its populations occur in seasonally flooding terrain (Luer 1975; Hágsater *et al.* 2005). On the other hand,

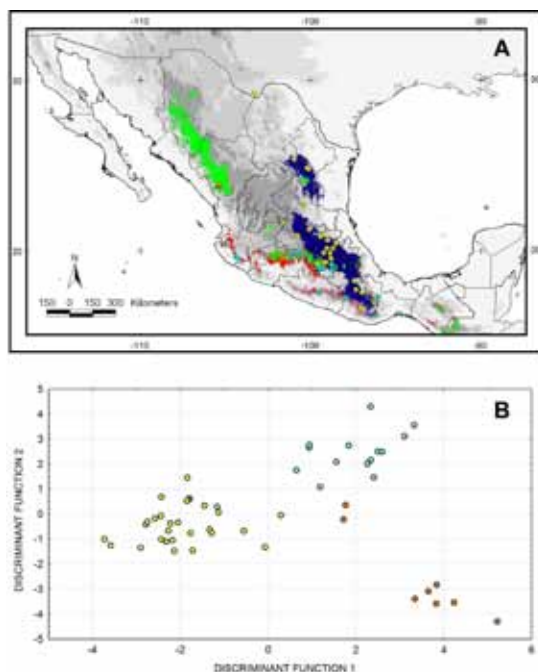


FIGURE 2. A. Potential distributions of *Sotoa* (“*Deiregyne*”) *confusa* (dark blue), *Schiedeella* (“*Deiregyne*”) *durangensis* (green), and *Svenkoeltzia* spp. (red) as inferred with Maxent; colored dots represent actual records of *Sotoa confusa* (yellow), *Schiedeella durangensis* (orange), and *Svenkoeltzia* spp. (pale blue). B. Plot of the discriminant function analysis; colored dots represent individual records of *Sotoa confusa* (yellow), *Schiedeella durangensis* (orange), and *Svenkoeltzia* spp. (pale blue) (see text).

D. confusa is found in a variety of habitats chiefly in semi-arid regions, including seasonally dry pine-oak and juniper-oak forest, tropical deciduous forest, various types of xerophilous scrub, and wastelands and induced pastures resulting from alteration of these plant associations (*e.g.*, Hágsater *et al.* 2005; Salazar *et al.* 2006; Salazar 2009; Peinado & Riojas 2008).

In all, the fact that *D. durangensis* and *D. confusa* represent two distinct species is now well established and they have been recognized as such in recent accounts of Mexican orchids (*e.g.*, Hágsater *et al.* 2005; Szlachetko *et al.* 2005; Soto *et al.* 2007). Nevertheless, their generic placement is a different matter. Taxonomists have included these two species either in *Deiregyne* (Garay 1982), *Schiedeella* (Schlechter 1920; Balogh 1982; Burns-Balogh 1986), or *Funkiella* (Szlachetko 1991, 1993; Szlachetko *et*

al. 2005), in all instances based on floral similarity. However, recent molecular phylogenetic studies have shown that floral morphology alone may not be a good indicator of phylogenetic relationship in some groups of Spiranthinae (Salazar *et al.* 2003; Górnaiak *et al.* 2006; Salazar & Dressler, submitted). In this work, the systematic position of *Deiregyne confusa* and *D. durangensis* is assessed by means of cladistic analyses of nucleotide sequences of two highly variable DNA markers, namely the region of the internal transcribed spacers of nuclear ribosomal DNA (nrITS; Baldwin *et al.* 1995; Álvarez & Wendel 2003) and plastid *trnL-trnF* region, which includes the intron of *trnL*, the intergenic spacer between *trnL* and *trnF*, and short exon portions (Taberlet *et al.* 1991; Kelchner 2000). Both these regions have been used previously, alone or in combination with each other and/or other DNA regions, for phylogeny reconstruction in Spiranthinae (Salazar *et al.* 2003; Górnaiak *et al.* 2006; Figueroa *et al.* 2008) and other orchidoid lineages (*e.g.*, Bellstedt *et al.* 2001; Clements *et al.* 2002; Bateman *et al.* 2003, 2009; van der Niet *et al.* 2005; Salazar *et al.* 2009; Álvarez-Molina & Cameron 2009).

We also evaluated the perceived differences in habitat preferences of *Deiregyne confusa*, *D. durangensis*, and, for reasons that will become evident later, *Svenkoeltzia congestiflora* and its kin, using geographic information systems (GIS) and niche modeling.

Materials and methods

Material studied. — Thirty-six species belonging to 21 genera of subtribe Spiranthinae *sensu* Salazar (2003) were analyzed, and representative species of subtribes Cranichidinae *s.l.*, Galeottiellinae, Goodyerinae, and Manniellinae were included as outgroups following previous phylogenetic studies (Salazar *et al.* 2003, 2009; Figueroa *et al.* 2008; Álvarez-Molina & Cameron 2009). A list of the taxa studied with voucher information and GenBank accessions is provided in Table 1.

Molecular methods. — Extraction, amplification, and sequencing of the DNA regions of interest were carried out using standard methods and primers described in Salazar *et al.* (2003). In all instances, bi-directional sequencing was performed and the chromatograms were edited and assembled with the program Sequencher (GeneCodes Corp.).

Phylogenetic analyses. — Alignment of the data matrices was done by eye and individual gap positions were treated as missing data.

All characters were treated as unordered and equally weighted. Parsimony analyses were conducted with the program PAUP* version 4.02b for Macintosh (Swofford 2002) for the nrITS region, the *trnL-trnF* region, and both regions in combination. Each analysis consisted of a heuristic search with 1000 replicates of random addition of sequences for the starting trees, branch-swapping using the “tree bisection-reconnection” (TBR) algorithm, and the option “MULTREES” was activated (to save multiple trees). All most-parsimonious trees (MPTs) were saved. Internal support for clades was assessed by nonparametric bootstrapping (Felsenstein 1985), in all cases consisting of 300 bootstrap replicates with heuristic searches, each including 20 random sequence additions for the starting trees and TBR branch-swapping. Up to 20 trees per bootstrap replicate were saved.

GIS and niche modeling. — Recently, several approaches to predictive modeling of the geographic distribution of species have been developed in a geographic information system (GIS) environment. Such modeling tools have been applied to problems in biogeography, conservation, evolutionary ecology, and ecological niche divergence among closely related species (*e.g.*, Ferrier 2002; Rice *et al.*, 2003; Kumar & Stohlgren 2009). In general, the procedure focuses on modeling ecological niches (the conjunction of ecological conditions within which a species is able to maintain populations without immigration; Grinnell 1917). Niche modeling uses environmental data and localities of occurrence of a species to produce a model of its requirements in those environmental/ecological dimensions (Stockwell & Peters 1999; Phillips *et al.* 2004), which is then projected on geographic space to create a map of the species’ potential distribution.

We assembled a database of 54 georeferenced herbarium records of *Deiregyne confusa*, *D. durangensis*, and *Svenkoeltzia* spp. based on the databases of two major collections of specimens of Mexican Orchidaceae, namely herbaria AMO and MEXU. In the last instance, records are publicly available through the portal of the Unidad de

Informática de la Biodiversidad (UNIBIO) of the Instituto de Biología, Universidad Nacional Autónoma de México (<http://unibio.ibiologia.unam.mx/>). We also incorporated records gathered in other herbaria, including AMES, K, ENCB, F, IEB, MEXU, MO, NY, SEL and US, as well as information from the literature. Subsequently, we used the Maximum Entropy modeling method (Phillips *et al.* 2004, 2006), as implemented in the software Maxent version 3.3.1 (freely available at <http://www.cs.princeton.edu/~schapire/maxent/>), to develop models of habitat suitability for the taxa. Maxent is a maximum entropy-based machine learning program that estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips *et al.* 2006). Besides data on species presence, distribution models require environmental variable layers; we included four topographic data (U.S. Geological Survey; <http://edcdaac.usgs.gov/gtopo30/hydro/>) and 19 bioclimatic parameters (including precipitation and temperature variables) with spatial resolution of 30 arc sec (~1 km²) (WorldClim dataset; Hijmans *et al.* 2005). To assess model performance, we used Receiver Operating Characteristic (ROC) curves. The main advantage of ROC analysis is that the area under the ROC curve (AUC) provides a single measure of model performance, independent of the choice of threshold (Phillips *et al.* 2006).

We performed a discriminant function analysis (DFA) using the software package STATISTICA 6.0 (Statsoft, Inc.) to elucidate the differentiation between the niches of the species. This multivariate analysis works in the space defined by the environmental predictors and compares the distribution of the species to one another. It computes the factor that maximizes the inter-species variance while minimizing intra-species variance and therefore represents the direction along which the species are most differentially distributed. Then we calculated the distance measures between the centroids of each species to determine the similarity/dissimilarity between them based on the Mahalanobis distance.

Since species' limits in *Svenkoeltzia* are unclear (see Salazar 2003; Soto *et al.* 2007), we pooled all the records of *Svenkoeltzia* spp. available to us as a single taxonomic unit for comparison with the habitat preferences of *Deiregyne confusa* and *D. durangensis*.

Results

Phylogenetic analyses. — The nrITS data set consisted of 771 characters, of which 241 (31%) were potentially informative to parsimony. The analysis of this region yielded six equally most parsimonious trees (MPTs) with a length of 977 steps, consistency index excluding uninformative characters (CI) = 0.46, and retention index (RI) = 0.65. The strict consensus of the six MPTs is shown in Fig. 3A. On the other hand, the *trnL-trnF* matrix encompassed 1653 characters, 216 (13%) of which were potentially parsimony-informative, and again six MPTs were found, these being 804 steps long, with CI = 0.53 and RI = 0.71. The strict consensus calculated from these is depicted in Fig. 3B. Both analyses recovered similar overall patterns of supported relationships, and there were no instances of contradictory clades with bootstrap percentages (BP) > 50.

The combined dataset of the nrITS and *trnL-trnF* regions consisted of 2424 characters, 457 (19%) of which were potentially informative to parsimony. The heuristic search found a single MPT with a length of 1790 steps, CI = 0.48, and RI = 0.67. The single tree recovered is depicted in Fig. 4. Spiranthinae (a-d) form a strongly supported monophyletic group (BP 100) and within them three major clades were recovered, which match the groups referred to as the *Stenorhynchos* (a; BP 95), *Pelexia* (b; BP 53), and *Spiranthes* clades (d; BP 100) by Salazar *et al.* (2003), plus an additional clade consisting of *Eurystyles* and *Lankesterella* (c; BP 100). The latter obtained high support (BP 90) as sister to the *Spiranthes* clade, but the *Pelexia* clade did not obtain a BP > 50 as the sister of [[*Lankesterella-Eurystyles*]-*Spiranthes* clade]]. The internal relationships of the *Stenorhynchos* and *Pelexia* clades mirror closely the results of Salazar *et al.* (2003) and will not be dealt with further here. In the case of the *Spiranthes* clade, our taxonomic sampling was more comprehensive than in that study. This clade consists of two weakly supported subclades, the first of which (BP 62) includes two strongly supported groups; in the first of them, *Schiedeella faucisanguinea* is sister to [*Microthelys minutiflora-Funkiella hyemalis*], whereas the second encompasses, on the one hand, [*Deiregyne confusa-Svenkoeltzia congestiflora*] (BP 98), and on the other hand *Beloglottis costaricensis* as the sister of monophyletic (and strongly supported) *Aulosepalum*. The other major subclade of the *Spiranthes* clade comprises *Spiranthes*

TABLE 1. Voucher information and GenBank accessions for DNA sequences.

Taxon	Voucher specimen	nrITS	<i>trnL-trnF</i>
Subtribe Cranichidinae			
<i>Ponthieva racemosa</i> (Walt.) Mohr	Mexico, <i>Salazar 6049</i> (MEXU)	AJ539508	AJ544490
<i>Prescottia plantaginea</i> Lindl.	Brazil, <i>Salazar 6350</i> (K)	AJ539511	AJ544493
Subtribe Galeottiellinae			
<i>Galeottiella sarcoglossa</i> (A.Rich. & Galeotti) Schltr.	Mexico, <i>Jiménez 2334</i> (AMO)	AJ539518	AJ544500
Subtribe Goodyerinae			
<i>Goodyera pubescens</i> (Willd.) R.Br.	USA, <i>Chase 212</i> (NCU)	AJ539519	AM419815
Subtribe Manniellinae			
<i>Manniella cyrpedioides</i> Salazar, T.Franke, Zapfack & Benkeen	Cameroon, <i>Salazar 6323</i> (YA)	AJ539516	AJ544498
Subtribe Spiranthinae			
<i>Autosepalum hemichreum</i> (Lindl.) Garay	Mexico, <i>Salazar 6044</i> (MEXU)	–	FN641878
	Mexico, <i>Soto 8336</i> (MEXU)	FN641866	–
<i>Autosepalum pyramidale</i> (Lindl.) M.A.Dix & M.W.Dix	Mexico, <i>Salazar 6061</i> (MEXU)	AM884872	FN641877
<i>Autosepalum tenuiflorum</i> (Greenm.) Garay	Mexico, <i>Salazar 6150</i> (MEXU)	AJ539591	AJ544474
<i>Beloglottis costaricensis</i> (Rehb.f.) Schltr.	Mexico, <i>Soto 8129</i> (MEXU)	AJ539492	AJ544475
<i>Coccineorchis cernua</i> (Lindl.) Garay	Panama, <i>Salazar 6249</i> (MEXU, spirit)	AJ539502	AJ544485
<i>Cyclopogon epiphyticum</i> (Dodson) Dodson	Ecuador, <i>Salazar 6345</i> (K)	AJ539499	AJ544482
<i>Deirygyne albobaginata</i> (C.Schweinf.) Garay	Mexico, <i>Jiménez 2164</i> (AMO)	FN641870	FN641882
<i>Deirygyne (Dithyridanthus) densiflora</i> (C.Schweinf.) Salazar & Soto Arenas	Mexico, <i>Salazar 6125</i> (MEXU)	FN641874	FN641886
<i>Deirygyne diaphana</i> (Lindl.) Garay	Mexico, <i>Salazar 6172</i> (MEXU)	AJ539484	AJ544467
<i>Deirygyne eriophora</i> (B.L.Rob. & Greenm.) Garay	Mexico, <i>Salazar 6104</i> (MEXU)	FN641873	FN641885
<i>Deirygyne falcata</i> (L.O.Williams) Garay	Mexico, <i>Salazar 6112</i> (MEXU)	FN641871	FN641883
<i>Deirygyne pseudopyramidalis</i> (L.O.Williams) Garay	Mexico, <i>Salazar 6126A</i> (MEXU)	FN641872	FN641884
<i>Deirygyne rhombilabia</i> Garay	Mexico, <i>Salazar 6138</i> (MEXU)	FN641869	FN641881
<i>Dichromanthus aurantiacus</i> (La Llave & Lex.) Salazar & Soto Arenas	Mexico, <i>Salazar 6351</i> (K)	AJ539485	AJ544468
<i>Dichromanthus cinnabarinus</i> (La Llave & Lex.) Garay	Mexico, <i>Linares 4469</i> (MEXU)	AJ539486	AJ544469
<i>Eltroplectris calcarata</i> (Sw.) Garay & H.R.Sweet	Brazil, <i>Soares s.n.</i> (MEXU, photograph)	AJ519448	AJ519452

<i>Eitroplectris triloba</i> (Lindl.) Pabst	Argentina, <i>Munich Bot. Gard.</i> 96/4474 (M)	FN641864	FN641875
<i>Eurystyles borealis</i> A.H.Heller	Mexico, <i>Soto 9149</i> (AMO)	AJ539497	AJ544480
<i>Funktiella hyemalis</i> (A.Rich. & Galeotti) Schltr.	Mexico, <i>Salazar 6128</i> (MEXU)	AJ539495	AJ544478
<i>Lankesterella gnoma</i> (Kraenzl.) Hoehne	Brazil, <i>Warren s.n.</i> (K)	FN556163	FN556168
<i>Mesadenella petenensis</i> (L.O. Williams) Garay	Mexico, <i>Salazar 6069</i> (MEXU)	AJ539503	AJ544486
<i>Mesadenus lucayanus</i> (Britt.) Schltr.	Mexico, <i>Salazar 6043</i> (MEXU)	AJ539488	AJ544471
<i>Microthelys minutiflora</i> (A.Rich. & Galeotti) Garay	Mexico, <i>Salazar 6129</i> (MEXU)	AJ539494	AJ544477
<i>Odontorrhynchus variabilis</i> Garay	Chile, <i>Wallace 130/85</i> (CANB)	AJ539498	AJ544481
<i>Pelexia adnata</i> (Sw.) Poit. ex Spreng.	Mexico, <i>Salazar 6012</i> (MEXU)	AJ539501	AJ544484
<i>Sacoila lanceolata</i> (Aubl.) Garay	Guatemala, <i>Förther 2545</i> (M)	AJ539504	–
	Brazil, <i>da Silva 874</i> (MG)	–	AJ544529
<i>Sarcoglotis acaulis</i> (J.E.Sm.) Schltr.	Trinidad, <i>Salazar 6346</i> (K)	AJ544483	AJ539500
<i>Schiedeella crenulata</i> (L.O. Williams) Espejo & López-Ferrari	Mexico, <i>Goldman 902</i> (BH)	FN641868	FN641880
<i>Schiedeella (Deiregyne) durangensis</i> (Ames & C.Schweinf.) Burns-Bal.	Mexico, <i>Soto 10673</i> (AMO)	FN641867	FN641879
<i>Schiedeella faucisanguinea</i> (Dod) Burns-Bal.	Mexico, Jiménez s.n. (AMO)	AJ539496	AJ544479
<i>Schiedeella llaveana</i> (Lindl.) Schltr.	Mexico, <i>Salazar 6105</i> (MEXU)	AJ539487	–
	Mexico, <i>Salazar 6073</i> (MEXU)	–	AJ544470
<i>Sotoa (Deiregyne) confusa</i> (Garay) Salazar	Mexico, <i>Hernández 3320</i> (MEXU)	FN641865	FN641876
<i>Spiranthes cernua</i> (L.) Rich.	USA, <i>Nickrent 4188</i> (MEXU)	AJ539489	AJ544472
<i>Spiranthes spiralis</i> (L.) Cheval.	UK, <i>Rudall & Bateman s.n.</i> (K)	AJ539490	AJ544473
<i>Stenorhynchos glitsteinii</i> E.A.Christ. ^a	Mexico, <i>Salazar 6090</i> (MEXU)	AJ539505	AJ544487
<i>Svenkoeltzia congestiflora</i> (L.O. Williams) Burns-Bal.	Mexico, <i>Salazar 6143</i> (MEXU)	AJ539493	AJ544476

^a Originally submitted to GenBank as "*Stenorhynchos speciosum*" and thus referred in Salazar *et al.* (2003).

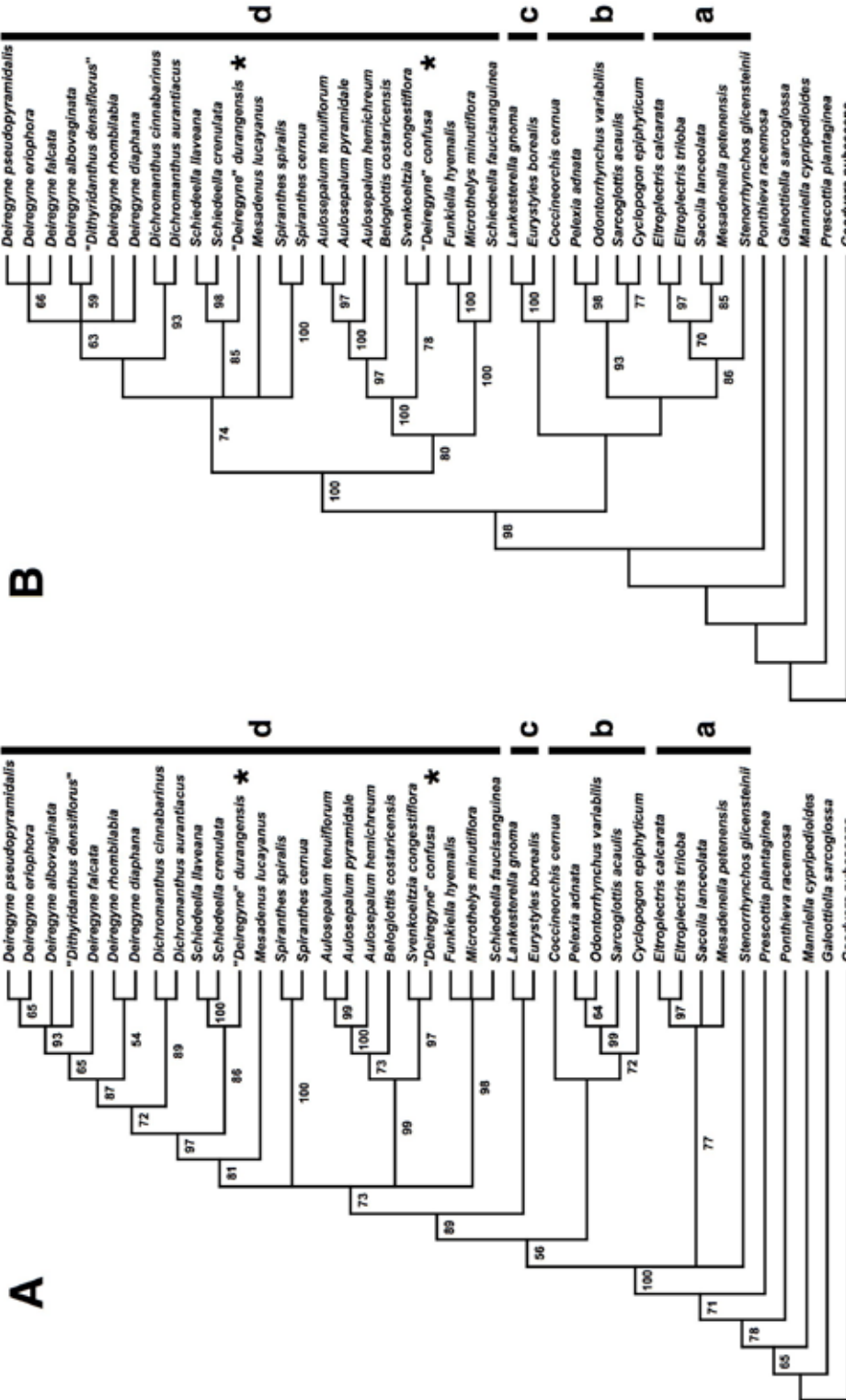


FIGURE 3. A. Strict consensus of the six MPTs found in the analysis of the nrITS region. B. Strict consensus of the six MPTs found in the analysis of the *trnL-trnF* region. Numbers below branches are bootstrap percentages. Bars marked with letters (a-d) refer to clades or groups discussed in the text. Asterisks mark the position of *Sotoa confusa* and *Schiedeella durangensis* in the trees.

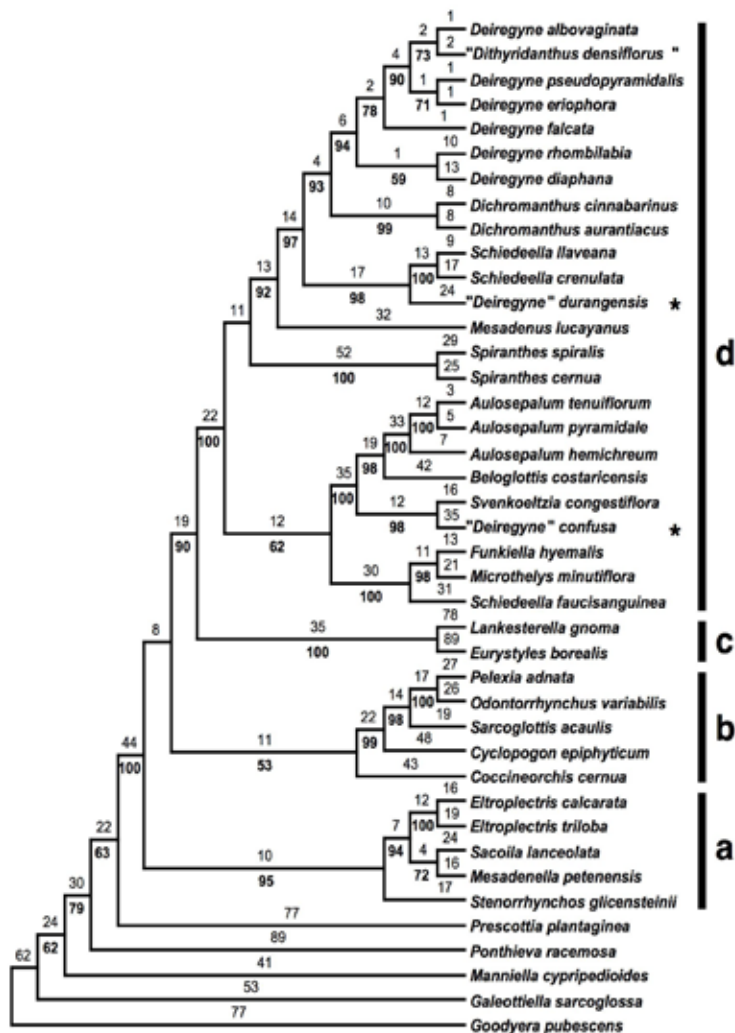


FIGURE 4. Single tree recovered in the analysis of combined nrITS and *trnL-trnF* DNA sequences. Numbers above branches are branch lengths, numbers below branches are bootstrap percentages. Bars marked with letters (a-d) refer to clades or groups discussed in the text. Asterisks mark the position of *Sotoa confusa* and *Schiedeella durangensis* in the trees.

(BP 100) as the sister of the rest (BP < 50), whereas *Mesadenus lucayanus* is strongly supported (BP 92) as sister to a clade encompassing [[*Deiregyne durangensis*-*Schiedeella crenulata*-*S. llaveana*]] in turn as the sister of *Dichromanthus* plus most species of *Deiregyne* (among which *Dithyridanthus densiflorus* is nested). All the internal relationships of these two groups are strongly supported. From Figs. 3-4 it is clear that neither *Schiedeella* nor *Deiregyne* is monophyletic.

Niche-modeling. — Distributional data are represented by 30, 15 and 9 unique localities for *Deiregyne*

confusa, *D. durangensis*, and *Svenkoeltzia* spp., respectively. Ecological niche models and associated distributional predictions developed for each species were all reasonably accurate; AUC values for all models are > 0.9, implying a potentially significant result. The potential ranges for the three taxa predicted by the models are shown in Fig. 2A. There is marginal overlap of the potential areas of *Svenkoeltzia* with those of *D. confusa* and *D. durangensis*, but they have never been found living sympatrically. These differences among the species are reflected also in the ecological distance measures that we calculated. According to the

Mahalanobis statistic (D2), the most similar taxa with respect to the environmental variables are *D. confusa* and *Svenkoeltzia* spp. (D2 = 18.78), whereas the most distinct are *D. confusa* and *D. durangensis* (D2 = 50.96). A plot constructed using individual scores on the two discriminant functions provides a picture of the pattern of segregation of the ecological parameters among the species investigated (Fig. 2B).

In the DFA, the first two discriminant functions are significant ($\lambda = 1$, $p < 0.0001$). The first and second discriminant functions explain 61.3% and 38.7% of the total variation of the sample, respectively. The most important environmental variables for group discrimination in the first function are precipitation of the rainiest period and precipitation of the warmest period, whereas for the second function they are basically temperature of the coldest month and temperature seasonality. The plot of the values of these functions recovers each taxon as a distinct cluster that can be characterized as follows: locations of *D. confusa* have low precipitation both during the rainiest period and the warmest period, intermediate temperature values for the coldest period, and intermediate seasonal temperature variation. *Deiregyne durangensis* occurs in locations where precipitation of the warmest period and temperature seasonality are higher, whereas *Svenkoeltzia* spp. are found in areas with higher precipitation during the rainiest period and with the lowest temperatures of the coldest period.

Discussion

The results of the present phylogenetic analyses show that "*Deiregyne*" *confusa* is only distantly related both to "*D.*" *durangensis* and to genuine members of *Deiregyne* as typified by *D. diaphana* (Lindl.) Garay (= *D. chloraeformis* (A. Rich. & Galeotti) Schltr.; see Garay 1982; Catling 1989; Salazar 2003; *contra* Balogh 1982; Burns-Balogh 1986, 1988; Szlachetko 1995). "*Deiregyne*" *durangensis* is strongly supported as member of a clade that includes the type species of *Schiedeella* (*S. llaveana* [Lindl.] Schltr. = *S. transversalis* Schltr.), and therefore could reasonably be included in *Schiedeella*, as in Hågsater *et al.* (2005) and Soto *et al.* (2007). We will refer to it as *Schiedeella durangensis* from here forth and the inclusion of this species does not significantly changes the circumscription of *Schiedeella* as interpreted by Salazar

(2003). The overall flower morphology of *Schiedeella* is similar to that of both *Deiregyne* and *Funkiella* but the former can be distinguished from these two genera by its herbaceous floral bracts that upon drying are scarious and opaque (vs. papery and translucent with contrasting dark veins) and the lack of orange-red to rust-red areas on the labellum, respectively. Our results also point to the polyphyly of *Schiedeella* as currently delimited because "*S.*" *faucisanguinea* (Dod) Burns-Bal. consistently groups with species of *Funkiella* and *Microthelys* (see below), sharing with them an affinity for high-montane habitats and the possession of red thickenings on the labellum (see Salazar 2003; Salazar *et al.* 2003). However, our present sampling of this clade is too sparse to sustain taxonomic changes at this time and this issue will be dealt with elsewhere (G.A. Salazar *et al.*, unpubl. data).

On the other hand, *Deiregyne* as interpreted here (following Garay 1982; Catling 1989; Salazar 2003) is the strongly supported sister of *Dichromanthus s.l.* (Salazar 2003; Salazar *et al.* 2002, 2003; Salazar & García-Mendoza 2009). The *Dichromanthus-Deiregyne* clade is sister to *Schiedeella*, in agreement with previous results of Salazar *et al.* (2003). Likewise, the nrITS analysis of Górnjak *et al.* (2006) recovered *Deiregyne diaphana* (as its synonym, *Burnsbaloghia diaphana* [Lindl.] Szlach.) in a strongly supported clade that also included *Dichromanthus* ("*Stenorrhynchos*") *aurantiacus* and *Schiedeella llaveana*. Although the present study included only seven of the twelve species we currently recognize in *Deiregyne* (Salazar 2003; cf. Soto *et al.* 2007), the species analyzed here represent a significant portion of the structural variation and the geographic distribution displayed by the genus and few future changes in its limits are anticipated.

"*Deiregyne*" *confusa*, henceforth referred to as *Sotoa confusa* (Garay) Salazar (see Nomenclature, below), did not group either with *Schiedeella* or with *Deiregyne*, being instead strongly associated with *Svenkoeltzia congestiflora* within a robust clade that also includes *Beloglottis* and *Aulosepalum*. The last whole group is in turn sister to a strongly supported *Funkiella* subclade encompassing *F. hyemalis*, *Microthelys minutiflora*, and, as noted earlier, *Schiedeella faucisanguinea*. These relationships might appear surprising at first sight, given the noticeable likeness in overall flower appearance of *Schiedeella*

durangensis and the species here referred to as *Sotoa confusa*. Nevertheless, as mentioned earlier, there are substantial differences in nectary structure and floral pubescence between these species and their similar outward appearance likely is an indication of similar pollination mechanisms. Both *Schiedeella durangensis* and *Sotoa confusa* possess a generalized suite of floral morphological traits likely related to pollination by nectar-foraging bees (e.g. *Bombus* spp.); these traits include white flowers with darker veins on tepals, a contrastingly colored area on the throat of the labellum, and diurnal floral scents (cf. Catling 1983; Salazar 2003). Indeed, pollination of *Schiedeella durangensis* by *Bombus steidachneri* Handrilsch, 1988 was recorded by Luer (1975) in the Estado de México. This pollination syndrome is also displayed by members of “true” *Deiregyne* (i.e. *D. diaphana* and its kin), *Schiedeella*, and *Funkiella*, and it might represent the plesiomorphic condition in the whole *Spiranthes* clade. In contrast, *Svenkoeltzia* encompasses one to four ill-defined species with bright yellow, tubular flowers on a more or less congested inflorescence (Burns-Balogh 1989; González 2000; Salazar 2003; Szlachetko *et al.* 2005), which are most likely pollinated by hummingbirds (Salazar 2003).

Ecological niche modeling substantiates the existence of noticeable differences in the ecological preferences of *Schiedeella durangensis* and *Sotoa confusa*, and their potential distributions inferred with Maxent do not overlap (Fig. 2A, B). In the case of *Svenkoeltzia*, there is marginal overlap with the distributions predicted for both *Sotoa confusa* and *Schiedeella durangensis*, but the potential overlap may be an artifact of the scale of the underlying cartography, since there are profound differences in their particular habitats. For instance, plants of *Svenkoeltzia* live epiphytically or on rocks in forests, whereas both *Schiedeella durangensis* and *Sotoa confusa* are geophytes occurring in open areas; as far as we now, none of them has ever been found occurring sympatrically with any other.

Garay (1982) envisioned monotypic genera as “[...] the inevitable, peripheral products of anagenesis, i.e., the evolutionary refinements within a main phylogenetic branch of the family [...]”. This logic applies to some extent in the case of *Sotoa confusa*, which, in spite of its close relationship to *Svenkoeltzia*,

differs from it in habitat preferences, flower structure, and (likely) pollination biology. Given their divergent natural histories, it seems to us less confusing to create a new genus for “*D.*” *confusa* than lumping it in an undiagnosable broader concept of *Svenkoeltzia*. The inclusion of *Sotoa confusa* and *Svenkoeltzia congestiflora* in *Funkiella*, as in Szlachetko (1991, 1993; also Garay 1982 in the case of *S. congestiflora*) is untenable on phylogenetic grounds, unless one is willing also to sink into *Funkiella* the morphologically distinctive genera *Aulosepalum* and *Beloglottis* (see Figs. 3, 4). There is no obvious advantage in lumping these ecologically, structurally and genetically distinctive clades, and therefore we opt here for erecting *Sotoa* as a distinct genus from *Svenkoeltzia*.

Nomenclature

***Sotoa* Salazar, gen. nov.**

Type species: *Sotoa confusa* (Garay) Salazar.

Morphologia tota floris et rostellis Deiregynae, Funkiellae et Schiedeellae similis; differt a tribus generibus fundo nectarii valde concavo-convexo, convexitate interna dense pubescenti, saepe apparenti ut crista longitudinali pubescenti in floribus siccis rursus madefactis; etiam differt a Deiregynae bracteae floralibus neque albidis translucidis neque venatione atrata; etiam differt a Funkiellae labello sine areis aurantiis vel ferrugineo-rubrescentibus.

This genus is named in honor of Miguel Angel Soto Arenas (1963-2009), outstanding contemporary botanist and leading expert on the Orchidaceae of Mexico. So far, *Sotoa* includes a single widespread species from semiarid regions of Mexico and southern USA:

***Sotoa confusa* (Garay) Salazar, comb. nov.**

Basionym: *Deiregyne confusa* Garay, Bot. Mus. Leaflet 28: 238. 1982. Holotype: Mexico. Hidalgo: lagoon of Metztlán, 1600 m, 27 March 1933, J. González [sic] & O. Nagel (sub E. Östlund) 2194 (AMES!).

Other synonyms: *Spiranthes confusa* (Garay) Kartesz & Ghandi, Phytologia 73: 128. 1992. *Schiedeella confusa* (Garay) Espejo & López-Ferrari, Phytologia 82: 80. 1997. *Funkiella durangensis* (Ames & C.Schweinf.) subsp. *confusa* (Garay) Szlach., Fragm. Flor. Geobot. 36: 20. 1991.

Funkiella confusa (Garay) Szlach., Rutkowski & Mytnik, Polish Bot. Stud. 20: 227. 2005.

As noted earlier, "*Dithyridanthus*" *densiflorus* is nested in *Deiregyne* (Figs. 3, 4) and is most closely related (and morphologically similar) to *Deiregyne albovaginata*. Thus the following new combination in *Deiregyne* is required to make classification consistent with its phylogenetic position.

Deiregyne densiflora (C.Schweinf.) Salazar & Soto Arenas, *comb. nov.*

Basionym: *Spiranthes densiflora* C.Schweinf., Bot. Mus. Leafl. 4: 104. 1937. Holotype: Mexico. Morelos: Tepeyte, 2300 m, flowered at Cuernavaca, 10 Oct. 1932, P. Carbonero (sub E. Östlund) 1513 (AMES!).

Other synonyms: *Schiedeella densiflora* (C.Schweinf.) Burns-Bal., Orquidea (Mexico City), n.s., 8: 39. 1981. *Dithyridanthus densiflorus* (C.Schweinf.) Garay, Bot. Mus. Leafl. 28: 316. 1982. *Stenorrhynchos densiflorus* (C.Schweinf.) Szlach., Fragm. Flor. Geobot. 37: 200. 1992 (as "*densiflora*").

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A NEW SPECIES OF *ODONTOGLOSSUM* (ORCHIDACEAE: ONCIDIINAEE) FROM ECUADOR

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ABSTRACT. A new and horticultural desirable species of *Odontoglossum* from Ecuador is described, illustrated and compared with similar species.

KEY WORDS: Ecuador, Orchidaceae, Oncidiinae, *Odontoglossum*, new species.

For many years commercial orchid business in Ecuador was limited to a few individuals' private enterprises, despite the richness of the orchid flora in the country. Not until Father Ángel Andretta, a Salesian missionary stationed in Ecuador and long time orchid enthusiast, together with the Portilla family established Ecuagenera did a more serious effort begin to create an efficient business model. The rest is history. Not only did Ecuagenera turn into a profitable commercial company, but it is also a most successful scientific contributor that has sponsored local education, conservation programs and research efforts by numerous visiting scientists and hobbyists with a passion for orchids. Untold new species have been discovered in this process and one of them is described in this paper.

Taxonomic treatment

Odontoglossum deburghraevianum Dalström & G.Merino, *sp. nov.*

TYPE: Ecuador. Azuay: Guarumales, 1700-2200 m, flowered in cultivation, Aug. 2000, *S. Dalström 2488-B* (holotype, QCNE). Fig. 1.

Odontoglossum harricano Rchb.f., et *Odontoglossum* helgae Königer similis, sed columnae tabula angulare infra stigma differt.

Plant epiphytic. *Pseudobulbs* caespitose, ovoid to pyriform, more or less compressed, becoming wrinkled with age, ancipitous, unifoliate or bifoliate,

ca 5—7 x 8—12 cm, subtended basally by 4 to 5 distichous sheaths, the uppermost foliaceous. *Leaves* conduplicate, subpetiolate, narrowly elliptic, or ovate to obovate, acute to obtuse, ca 18—40 x 3—5 cm. *Inflorescence* erect to arching, almost straight, 3 to 7 flowered, to ca 35 cm long raceme; bracts appressed, scale-like, acute 3—10 mm long. *Pedicel* with *ovary* 35—50 mm long. *Flowers* more or less stellate to slightly campanulate, with recurved apices; *dorsal sepal* whitish to pale yellowish, almost entirely covered by large irregular brown blotches and markings, ovate to broadly elliptic, obtuse and slightly apiculate, more or less undulate, 35—38 x 15—20 mm; *lateral sepals* similar in color, slightly spatulate and weakly oblique, ovate, obtuse and slightly apiculate, variably undulate, 35—42 x 14—16 mm; *petals* similar in color, often less spotted basally, ovate to broadly elliptic, acute to slightly acuminate, variably undulate and sometimes slightly oblique, 35—40 x 12—14 mm; *lip* basally pale yellow, then white, heavily marked and spotted with purple, particularly on the lower part of the lamina, rigidly adnate to the base of the column, then 90° angled downward from the column, unguiculate with erect basal, lateral, fleshy lobes, then with a broadly pandurate and undulate lamina, with lower, lateral auriculate lobes, and a broad, widely undulate, apically involute retuse to rounded, sometimes apiculate apex; callus of a fleshy, slightly pubescent distinctly and narrowly canaliculated, longitudinal structure, emerging basally and diverging apically into unequally sized irregularly denticulate, fleshy keels, sometimes

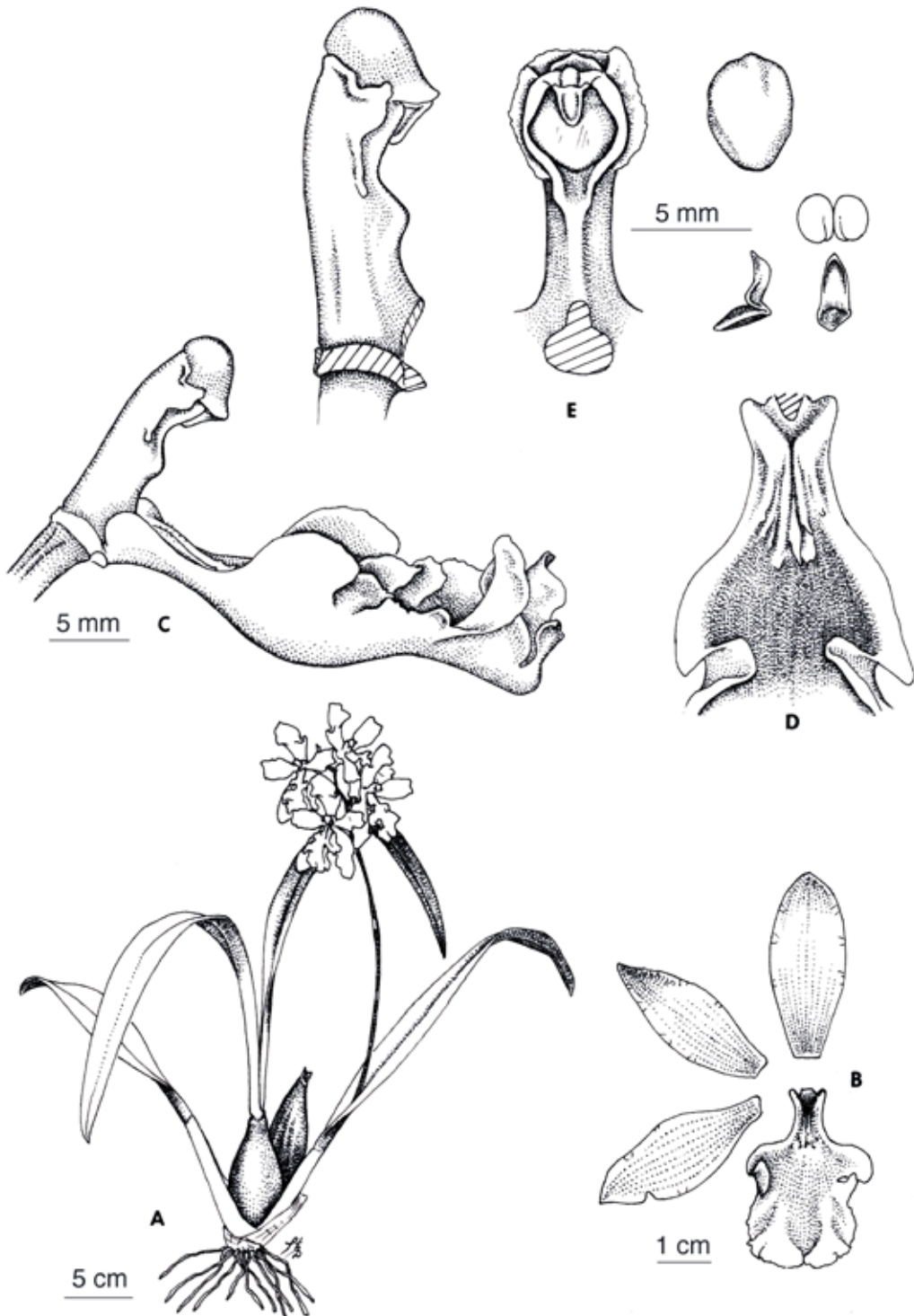


FIGURE 1. *Odontoglossum deburghraevianum*. A: plant habit. B: dissected flower. C: column and lip, lateral view. D: base of lip, dorsal view. E: column, lateral and ventral view, anther cap and pollinaria.

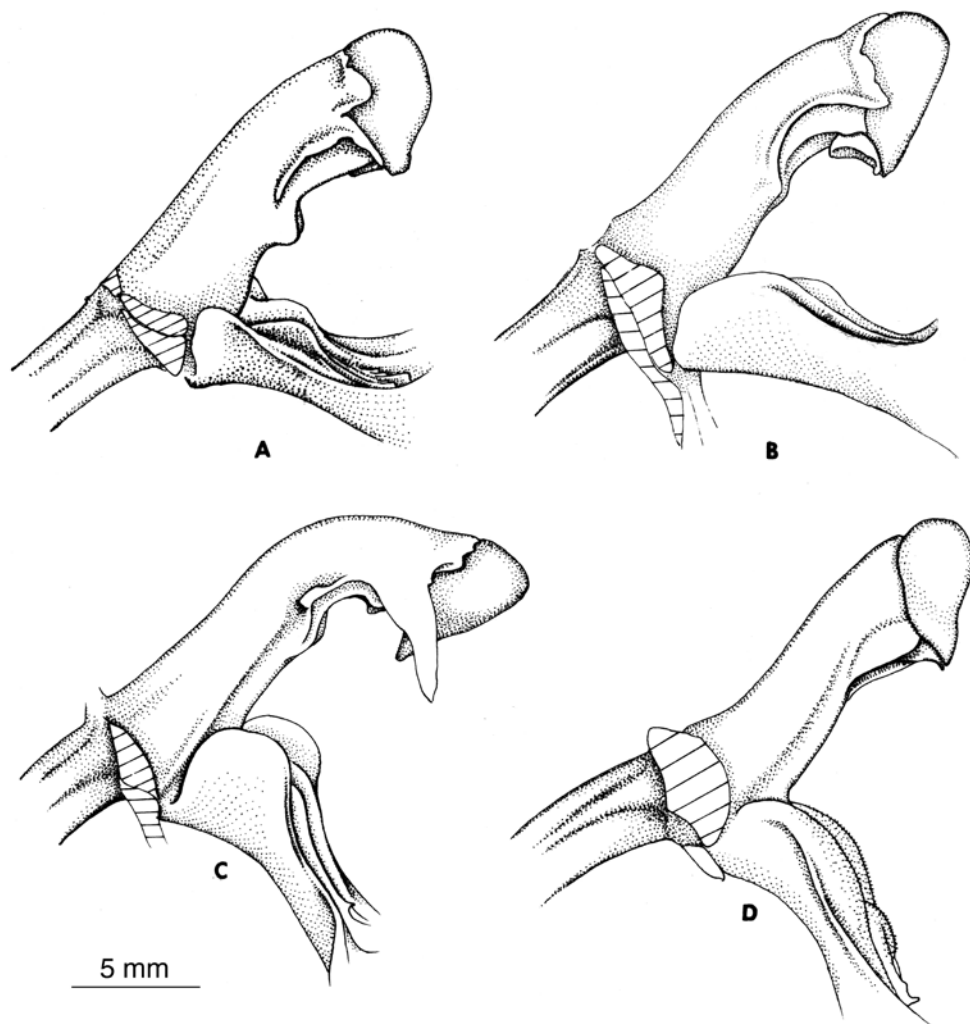


FIGURE 2. Column and base of lip, lateral views, A — *Odontoglossum deburghraevae*. B — *O. harryanum*. C — *O. wyattianum*. D — *O. helgae*.

with additional, variably sized denticles, extending to ca $\frac{1}{4}$ -th of the length of the lip; *column* erect and apically slightly curved towards the lip, basally terete, with a ventral, longitudinal fleshy ridge, diverging into a broader, canaliculated tabula infrastigmatica, and with variable, serrate lateral wings and apical hood, ca 13 mm long; *anther cap* more or less globular with a slight dorsal knob or ridge; *pollinarium* of two globose to pyriform, cleft pollinia on an oblong triangular ca 2.5 mm long stipe, on an elliptic, pulvinate viscidium.

Odontoglossum deburghraevae differs from the rather similar *Odontoglossum harryanum*

Rchb.f. (Fig. 2B) by the smaller flower with a more open appearance, and the narrower base of the lip, in addition to the distinct ventral angles on the column of the former. The flower of *Odontoglossum wyattianum* A.G. Wilson (Fig. 2C) differs in having a column that is distinctly curved towards the lip and with well-developed, broadly falcate apical wings. The flower of *Odontoglossum helgae* Königer (Fig. 2D) has a more erect and terete column without any ventral angles. The flowers of the much smaller *Odontoglossum velleum* Rchb.f., are altogether different with a short and straight column that is parallel with the base of the lip.

The first examined evidences of *Odontoglossum deburghgraeveanum* are two color slides in the collections of the former Orchid Identification Center at the Marie Selby Botanical Gardens, Sarasota, Florida, labeled “*Odm. wyattianum?*”. One slide is from the Lee Kuhn collection and is probably from a plant that flowered at J & L Orchids in Connecticut at some time, but the second slide is of unknown origin (possibly from Gilberto Escobar’s extensive slide collection) and was processed in August 1973. Father Andreetta has since collected some additional plants of this species apparently near the little town of Guarumales, Ecuador, in 1992. In August of 2000, plants of this species were in bloom at Ecuagenera’s nursery in Gualaceo, where they were offered for sale, marketed as *Odm. helgae* Königer, but a comparison with the type of that species and with most recently discovered additional plant material in northern Peru, reveal that they represent separate taxa due to distinct morphological differences.

Odontoglossum deburghgraeveanum has apparently been collected on few occasions in an area where the closely related *Odm. harryanum* and *Odm. velleum* Rchb.f., also occur sympatrically and the possibility of *Odm. deburghgraeveanum* being a natural hybrid between the other two has been considered. Although similar in coloration, the morphological differences between the three species suggest that a hybrid origin is not likely. The column structure and the base of the lip in particular are quite defined and consistently different for the three species. *Odontoglossum deburghgraeveanum* is rather variable in coloration, as most species in the genus, which is a factor that often deceives collectors and scientists alike to believe they see different species (or natural hybrids), and presumably also deceives pollinators as well to see different types of flowers where some awards eventually can be obtained. This topic has been discussed in a separate article (Dalström, 2003).

ETYMOLOGY: Named in honor of Guido Deburghgraeve MD., of Liedekerke, Belgium, a passionate grower of *Odontoglossum* and plants of related genera, who has contributed substantially to the knowledge and understanding of how to view and classify these very complex and troublesome orchids.

ADDITIONAL SPECIMENS SEEN: Aug. 1973, color transparency (SEL); Azuay: Guarumales 1700–2000 m, 1992, *A. Andreetta s.n.* (fide G. Merino, voucher not preserved); flowered in cultivation at Ecuagenera, Aug. 2000, *S. Dalström 2488-A* (SEL).

DISTRIBUTION: *Odontoglossum deburghgraeveanum* is currently reported from one locality in east-central Ecuador. It is likely to be found elsewhere, however, because many species of *Odontoglossum* occur in very “spotty” populations, often over a very large area and are considered rare until another population suddenly is discovered quite some distance away. To make matters worse, sometimes plants are purchased from private collectors where the original locality may be lost or falsified.

IN MEMORIAM: The authors are deeply saddened by the abrupt and premature death of one of Mexico’s finest orchid scientists. Miguel Ángel Soto Arenas will be long remembered for his substantial scientific contributions even among those of us who never had the pleasure of knowing him in person.

ACKNOWLEDGEMENTS. The authors wish to thank Carl Luer for help with the Latin diagnosis.

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**A NEW *ORNITHIDIUM* (ORCHIDACEAE: MAXILLARIINAE)
FROM THE MASSIF DE LA HOTTE OF HAITI**

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ABSTRACT. A new species of *Ornithidium* from the Massif de la Hotte, one of the last remaining orchid-rich regions of Haiti, is described and illustrated. Collected in the 1980s by Donald D. Dod whose original specimen has been lost and whose live plants only just recently flowered, the new species is closely related to *O. coccineum* based on both morphology and molecular sequences. It is distinguished from the latter by shorter apical leaves, globose pseudobulbs and longer sepals.

KEY WORDS: Greater Antilles, Orchidaceae, *Ornithidium*, Haiti, Donald D. Dod, orchid flora

In the mid 1980s, when Donald D. Dod (1912–2008) was working at the Jardín Botánico Nacional “Rafael Mosocoso” in Santo Domingo, Dominican Republic, he visited Pic Macaya National Park in the Massif de la Hotte, Haiti, with a scientific team from the University of Florida led by Walter S. Judd (see Dod 1984a,b, 1992, Dod & Judd 1986, Judd 1987). Don was an extraordinary orchid collector. His meticulous field habits resulted in the discovery of numerous new species, many of which were small-flowered, inconspicuous pleurothallids. Some of the plants that he had collected from the trip to Pic Macaya National Park still exist in cultivation. One of them remained healthy but had been reluctant to flower. Don thought that it might be *Ornithidium croceorubens* Rchb.f. (Dod 1984b, Dod & Judd 1986). The type of *O. croceorubens* hails from northern Haiti (Pic Macaya is in southwestern Haiti). It had been collected by L. C. Richard in the 19th century, but the species had not been collected on the island since. Nobody paid much attention to it until Nir (2000) located the type at W and published a sketch of the flower and habit. We now regard *O. croceorubens* to be a synonym of *Ornithidium inflexum* (Lindl.) Rchb.f. As a consequence of our better understanding of *O. croceorubens*, it became abundantly clear that Don’s plant was not what Nir had drawn, leaving Don’s *Ornithidium* species without a nomenclatural home.

Several years ago Don graciously gave us a piece of his plant so that we could do some DNA sequence analyses at the University of Florida. Our plant died without flowering, but we did manage to amass enough sequence data to suggest that it was sister to *Ornithidium coccineum* (Jacq.) R.Br. After that, we shelved the problem hoping that Don’s plants would flower.

Recently, as one of us (JDA) was wrapping up the Orchidaceae treatment for the Flora of the Greater Antilles (Ackerman in press), we decided to check on the status of Don’s plant, hoping for more material. By this time, Don reached his 90’s and it was time for changes so he transferred his live collection of plants to the University of California Botanical Garden in Berkeley where after about a year, the *Ornithidium* flowered! With the help of UCBG’s Holly Forbes, we not only received additional material for more thorough sequencing but also pickled flowers to describe. Herein we propose this species as new to science and show its phylogenetic position within the Maxillariinae (generic concepts according to Blanco *et al.* 2007).

***Ornithidium donaldeenodii* Ackerman & Whitten, sp. nov.**

TYPE. HAITI: Dept. du Sud, Massif de la Hotte, Pic Macaya National Park, Formond, 18°22’57”N 73°59’57”W, discovered by Donald D. Dod, flowered

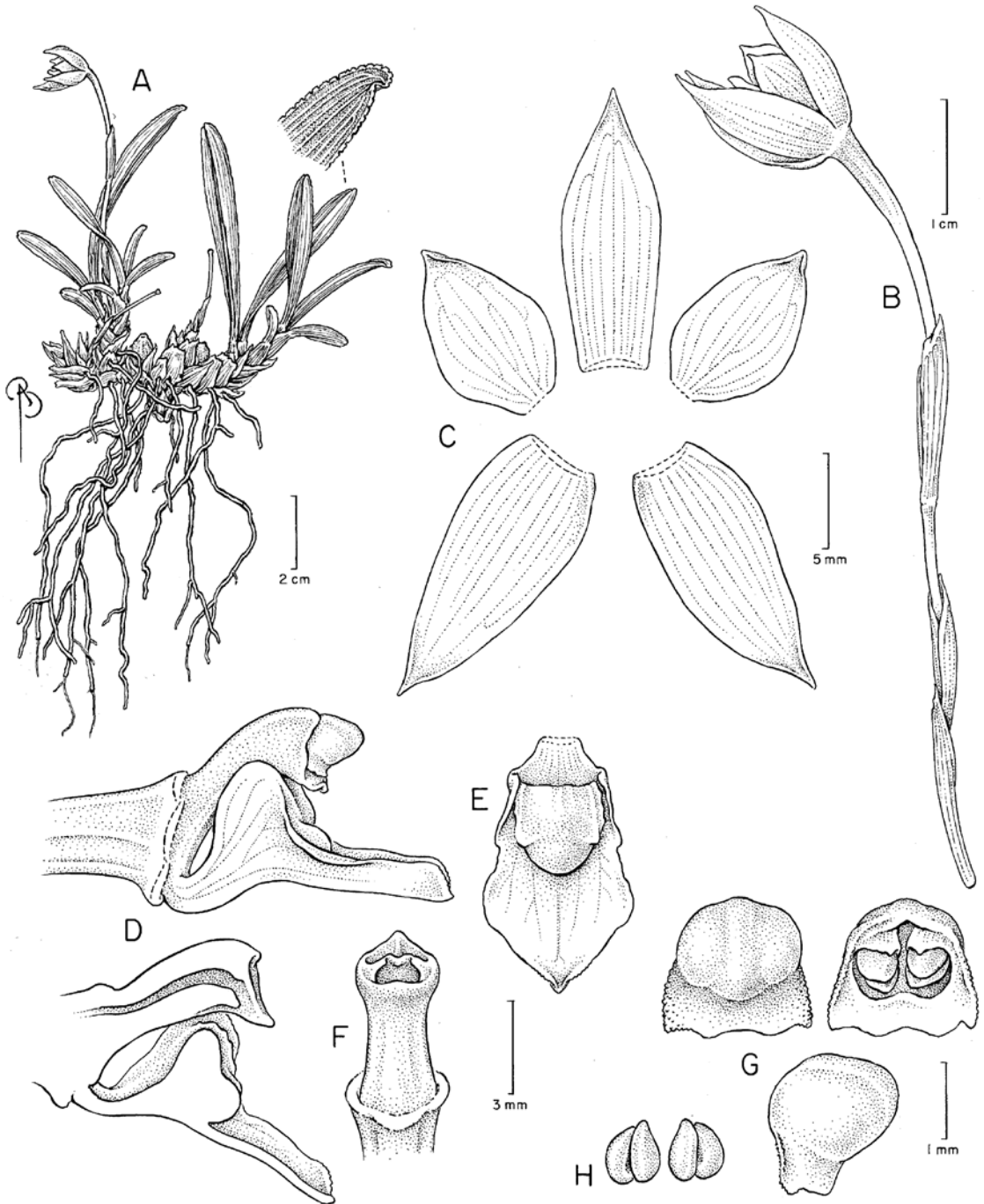


FIGURE 1. *Ornithidium donaldeadodii* Ackerman & Whitten. A — Plant habit. B — Inflorescence, side view. C — Perianth parts: dorsal sepal, lateral petals and lateral sepals. D — Column and lip, side view and longitudinal section. E — Lip, dorsal view. F — Column without anther, ventral view. G — Anther, dorsal (left), ventral (right) and lateral views. H — Pollinia. (Drawn from the holotype.) Illustrated by Bobbi Angell.

in cultivation at the University of California Botanical Garden, Berkeley, 8 May 2009, *H. C. Forbes s.n.* (holotype, UC; isotype, UPRRP). Fig. 1.

Usage synonym: *Maxillaria croceorubens* auct. non (Rech.f.) L.O. Williams: *Dod in Moscosoa* 3: 94, 102. 1984.

Ornithidium coccineum aemulans, differt foliis apicalibus brevibus sepalis longis et pseudobulbis globosis.

Epiphytic, caespitose herbs. *Roots* numerous, velamentous. *Pseudobulbs* green, slowly turning brown with age, globose, smooth, 1.0-1.5 cm diam., subtended by two foliaceous bracts. *Leaves* 1 from apex of pseudobulb, thin, ligulate, rounded-retuse, minutely crenulate at apex, slightly asymmetrical, 5-10 cm long, 6-10 mm wide, subtending pseudobulb bracts foliaceous and sometimes longer than apical leaf. *Inflorescences* one to several from new shoots, scapes ca. 10-11 mm long, single-flowered; floral bract scarious, brown with a hyaline apical margin, tightly sheathing the pedicellate ovary at base, inflated and loosely sheathing above, truncate, apiculate, 15 mm long. *Flowers* bright red to red-orange, campanulate; pedicellate ovary straight, 35-37 mm long, 1.3 mm diam. at apex of floral bract, 2.5 mm diam. below the perianth; sepals similar, dorsal sepal concave-to subcanaliculate, broadly elliptic-ovate, apically thickened, acuminate, 14-16 mm long, 5.5 mm wide at base, 6.6 mm wide near the middle when spread, lateral sepals slightly concave, ovate, acute and narrowing and thickening to a subacuminate apex, 15-16 mm long, 4.5 mm wide at base, 6.2 mm wide near the middle; petals slightly concave, broadly elliptical, abruptly acute with a slightly thickened apex, 9.5-10 mm long, 2 mm wide at base and 5-6 mm at the middle; labellum very fleshy, rigidly attached to the column foot, trilobed, slightly geniculate, ca. 7.5 mm long, claw concave, ca. 1 mm long, lateral lobes erect, just reaching the sides of the column to flank the stigma, convex, oblong, rounded, 3.5 mm long, 2 mm wide, mid lobe ovate, acute, somewhat flat, 5 mm long, 4 mm wide, callus yellowish, nearly filling the space between the lateral lobes, spilling glacier-like down to the base of the mid lobe ending in a minutely warty, rounded bump; column semiterete, erect, arched just

below stigma, 4.5 mm long measured dorsally (less anther cap), 6 mm long measured ventral from the tip of the column foot to the rostellum, 2 mm diam. at the base, 1.7 mm diam. just below the stigma, 2.4 mm diam. across the deeply concave stigma, pollinia 4, flattened, ovate. *Fruits* unknown.

ETYMOLOGY: Named in honor of "Don" Donald D. Dod (see Jiménez 2003) whose name graces numerous species of Hispaniolan orchids, but none in this form. After a long and fulfilling journey, Don died in 2008.

We compared photographs and pickled flowers of *O. donaldeenodii* from the University of California Berkeley Botanical Garden collection to fresh, pickled and pressed specimens of *O. coccineum* from the UPRRP herbarium (DOMINICAN REPUBLIC: Prov. San Cristóbal, Cordillera Central, *Jimenez, Mejia, & Veloz 1362*; Prov. Barahona, Sierra Baoruco, *Ackerman, Williams, Tremblay & Higgins 3294*; Prov. La Vega, Reserva Científica Ebano Verde, *Ackerman, Carromero & Dod 2941*; PUERTO RICO: Mun. Barranquitas, Cerro La Torrecilla, *Ackerman 2360*; *Ackerman & Zimmerman 2674*; *Axelrod & Ackerman 746*; *Rodríguez 16*; Mun. Ponce, Toro Negro Forest Reserve, *Axelrod & Chavez 4327*; Mun. Patillas, Carite Forest Reserve, *Axelrod 7632*; Tropic Ventures, *Taylor & Scott 7411*; Mun. San Lorenzo-Patillas, Carite Forest Reserve, *Axelrod & Gust 12962*; Mun. Río Grande, Luquillo Mountains, *Ackerman & Montalvo 1644*; *Ackerman & Ackerman 4216*; *Axelrod, Ackerman & Zimmerman 4395*; *Ackerman 4494*; *García Ruiz 14*; Mun. Naguabo, Luquillo Mountains, *Ackerman, Gaa, Montalvo & Parrilla 1820*; *Axelrod, Fritsch & Santiago 12551*; Mun. Río Grande-Naguabo, Luquillo Mountains, *Ackerman 1930*). Dod (1984b) cited his collection, *Dod 906*, at JBSD, but Francisco Jiménez of JBSD was unable to locate it for us.

The flowers of *Ornithidium donaldeenodii* are similar to *O. coccineum* in both color and form. The two species differ in at least the following characteristics. The apical leaves of *O. donaldeenodii* are rather short, 5-10 cm long, whereas those of *O. coccineum* are very rarely as short as 10 cm and reach to 45 cm in length. Lateral sepals of the former are about 16 mm long while those of the latter are 11-12.5 mm long, at least in the Greater Antilles. While the more familiar *O. coccineum* has dark green pseudobulbs that are distinctively compressed

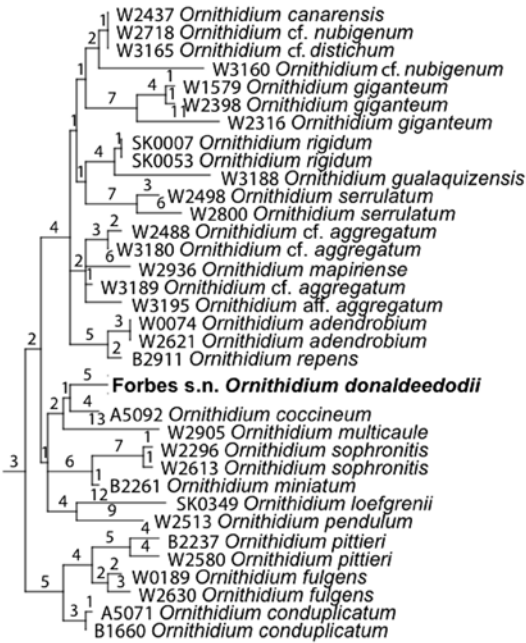


FIGURE 2. A molecular phylogeny of *Ornithidium* including *O. donaldehydii* based upon parsimony analyses of nrITS sequences; analyses are adapted from those of Whitten *et al.* 2007. Numbers above branches are branch lengths.

laterally and wrinkle with age, those of *O. donaldehydii* are a light green, globose, smooth and do not appear to darken and wrinkle with age. Dod (1984b) contradicts our description in the length of the sepals and we can only say that he must have gotten the differences reversed. The flowers are slightly more compressed laterally but one must have both species in hand to see that. He also mentioned that this species has tightly caespitose pseudobulbs, which is true, but the pseudobulbs of young flowering plants of *O. coccineum* are like that as well. For detailed descriptions of *O. coccineum*, see Ackerman (1995, in press) and Nir (2000).

To assess its phylogenetic distinctiveness and placement within *Ornithidium*, we sequenced two accessions of *O. donaldehydii* (probably divisions of the type material) for the nrITS DNA region, following protocols and data matrix in Whitten *et al.* 2007. The resulting sequences are identical. GenBank numbers are GU177874 *Forbes s.n.* (UC) and GU177875 *Whitten 3593* (FLAS). The resulting cladogram (Fig. 2) confirms its placement within *Ornithidium* Salisb. ex R. Br. and its distinctiveness from *O. coccineum*.

ACKNOWLEDGEMENTS. The authors thank the ghost of Donald D. Dod for providing us with samples of his *Ornithidium*, and Holly Forbes for her help at the UC Botanical Garden. Bobbi Angell did the drawing for which we are very grateful. Mario Blanco reviewed the manuscript for which we are appreciative. We also thank Francisco Jiménez who had searched JBSD for *Dod 606*. Funding was provided by U.S. National Science Foundation grants No. DEB-0234064 to N. H. Williams and W. M. Whitten, and No. HRD-0734826 to E. Cuevas. Additional funding was provided by a Furniss Foundation graduate student fellowship from the American Orchid Society to M. A. Blanco and by Kew Latin American Research Fellowships to M. A. Blanco.

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NOVELTIES IN THE ORCHID FLORA OF VENEZUELA II — CRANICHIDEAE*

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ABSTRACT. Two new orchid species in tribe Cranichideae, collected in the context of the project “Flora de Orquídeas de los Estados Amazonas y Bolívar, Venezuela” (Orchid Flora of Amazonas and Bolívar states, Venezuela) are described and illustrated. *Ligeophila gavilanensis* (subtribe Goodyerinae) is similar to *L. unicornis* but differs in having broader (1.75—2.90 versus 0.93—1.50 cm) narrowly elliptic to oblong-lanceolate (not lanceolate) leaves, flowers with oblong-lanceolate, obtuse (not broadly lanceolate, acute) epichile lobules, and an unappendaged (i.e., lacking an oblong, compressed projection) epichile. *Sarcoglottis maroaënsis* (subtribe Spiranthinae) is similar to *S. metallica* but the new species differs in the cream flowers with dark reddish veins in the sepals, petals, and labellum, and the leaves of different color. In flower color it is similar to *S. ventricosa* but the inflorescence of *Sarcoglottis maroaënsis* is more lax and not lanate, the flowers are smaller, and the lateral sepals and labellum are different. We report an isotype of *Sarcoglottis stergiosii* not cited in the protologue and a specimen collected in the Colombian Amazon.

RESUMEN. Se describen e ilustran dos nuevas orquídeas en la tribu Cranichideae colectadas en el contexto del proyecto “Flora de orquídeas de los estados Amazonas y Bolívar, Venezuela”. *Ligeophila gavilanensis* (subtribu Goodyerinae) es similar a *L. unicornis* pero difiere por sus hojas más anchas (1.75—2.90 versus 0.93—1.50 cm), angostamente elípticas hasta oblongo lanceoladas (no lanceoladas) y flores con los lóbulos del epiquilo oblongo-lanceolados, obtusos (no anchamente lanceolados, agudos) y un epiquilo sin apéndice (careciendo de una proyección oblonga, comprimida). *Sarcoglottis maroaënsis* (subtribu Spiranthinae) es similar a *S. metallica* pero la nueva especie difiere por las flores color crema con venas rojizo oscuro en los sépalos, pétalos y labelo y por las hojas de color diferente. En color floral es similar a *S. ventricosa* pero las inflorescencias de *Sarcoglottis maroaënsis* son más laxas y no lanadas, las flores son menores y los sépalos laterales y el labelo son diferentes. Reportamos un isotipo de *Sarcoglottis stergiosii* no citado en el protólogo, así como un espécimen colectado en la Amazonía colombiana. También se incluye una clave para identificar las especies de *Sarcoglottis* reportadas para la Guayana venezolana.

KEY WORD / PALABRAS CLAVE: Amazonas, Bolívar, Guayana, *Ligeophila*, *Sarcoglottis*, Venezuela

The following two new species of Orchidaceae (Cranichideae) were collected in the context of the project “Flora de orquídeas de los estados Amazonas y Bolívar, Venezuela” (Orchid flora of Amazonas and Bolívar state, Venezuela”).

Subtribe Goodyerinae Kl. (Garay, 1977, *pro parte*; Ormerod & Cribb, 2003: 64).

Ligeophila Garay (Garay, 1977; Ormerod & Cribb, 2003: 114; Ormerod, 2009).

Ligeophila gavilanensis Ormerod & G. A. Romero,
sp. nov.

TYPE: VENEZUELA. Amazonas: Municipio Autónomo

* The first article in this series was published in Harvard Pap. Bot. 14 (2): 203—211. December 2009.

Atures, río Gavilán, margen derecha (oeste) del río en las cercanías del raudal Gavilán,” 120 m, 8 November 1996, “hierba terrestre, hojas verde-marrón con vetas longitudinales verdes, flores blancas, localmente frecuente pero pocos individuos en flor,” G. A. Romero. *L. M. Campbell & C. Gómez 3066* (holotype: VEN; isotypes: TFAV, fragment AMES). FIG. 1A—B, 2.

Affinis *Ligeophilae unicorni* Ormerod, sed folia latiora ex anguste elliptico oblongo-lanceolata (non lanceolata), flores epichili lobulis oblongo-lanceolatis, obtusis (non late lanceolatis, acutis).

Terrestrial, erects *herbs*. *Rhizome* terete, rooting at nodes, lower half creeping, upper half erect, ca. 10.5 cm long; internodes 0.5—1.6 x 0.15—0.30 cm. *Stem* erect, laxly 4—5-leaved, ca. 10 cm long; internodes 1.35—3.20 x 0.2—0.3 cm. *Leaves* obliquely narrowly elliptic to oblong-lanceolate, subacuminate, margins undulate, green-maroon, 5.3—9.2 x 1.75—2.90 cm; petiole and sheath 0.9—2.6 cm long. *Inflorescence* terminal, pubescent, ca. 6.1 cm long; peduncle ca. 3.1 cm long; sheathing bracts 3, overlapping, 1.5—1.8 cm long; rachis subdensely-flowered, ca. 3 cm long; *floral bracts* ovate-lanceolate, acute, to 13 x 5 mm. Pedicellate ovary cylindrical, pubescent, ca. 10 mm long. *Flowers* resupinate, externally pubescent. *Dorsal sepal* reddish-brown, ovate-lanceolate, truncate, shallowly concave, 7.6 x 3.2 mm. *Lateral sepals* green toward the base, reddish apically, obliquely oblong-lanceolate, obtuse, 8 x 2.5 mm. *Petals* white, with a medial reddish-black oblanceolate stripe, obliquely obovate-oblanceolate, acute, forming a hood with the dorsal sepals, 6.75 x 2.8 mm. *Labellum* white, spurred, trilobed, joined to the ovary and to the column for ca. 2.0 mm; spur clavate, apex shortly obtusely bilobed, 6.5 mm long; hypochile in total ca. 3.8 mm long, ca. 4.2 mm wide, each side with a semiorbicular lobe 2.1 mm wide, terminating in an obliquely triangular extension directed forward and outward, outside each side with a fleshy patch upon a convexity (mirrored by an internal concavity); mesochile obtuse, ca. 1.75 mm long, basally ca. 1 mm wide, apex ca. 1.5 mm

wide; epichile hippocrepiform, reflexed, with lobules pointing forward, medially 2.8 mm long, 6 mm wide, lobules oblong-lanceolate, obtuse, falcate, ca. 7.75 mm long from epichile tip to apex. *Column* with an elongate basally flexible rostellum, in total 5 mm long (description based on a dry specimen and flowers preserved in alcohol).

ETYMOLOGY: Named after the type locality, Caño Gavilán, a small clear-water river that joins the Cataniapo river just west of the Huottuja (Piaroa) community of Gavilán.

DISTRIBUTION: So far known only from the type locality.

Ligeophila gavilanensis appears to be most closely related to *L. unicornis* Ormerod, also from Venezuela, both species having a labellum hypochile with similar sidelobes. From the latter, however, the new species differs in having broader (1.75—2.90 versus 0.93—1.50 cm) narrowly elliptic to oblong-lanceolate (not lanceolate) leaves, and flowers with oblong-lanceolate, obtuse (not broadly lanceolate, acute) epichile lobules, and an unappendaged (i.e., lacking an oblong, compressed projection) epichile. Another species with a similarly shaped labellum hypochile is *L. jamesonii* Garay, from Colombia and Ecuador. The latter has a much larger inflorescence (rachis > 11 cm long) of many more flowers and somewhat obliquely rhombic (not obliquely obovate-oblanceolate), narrower (1.5 versus 2.8 mm) petals.

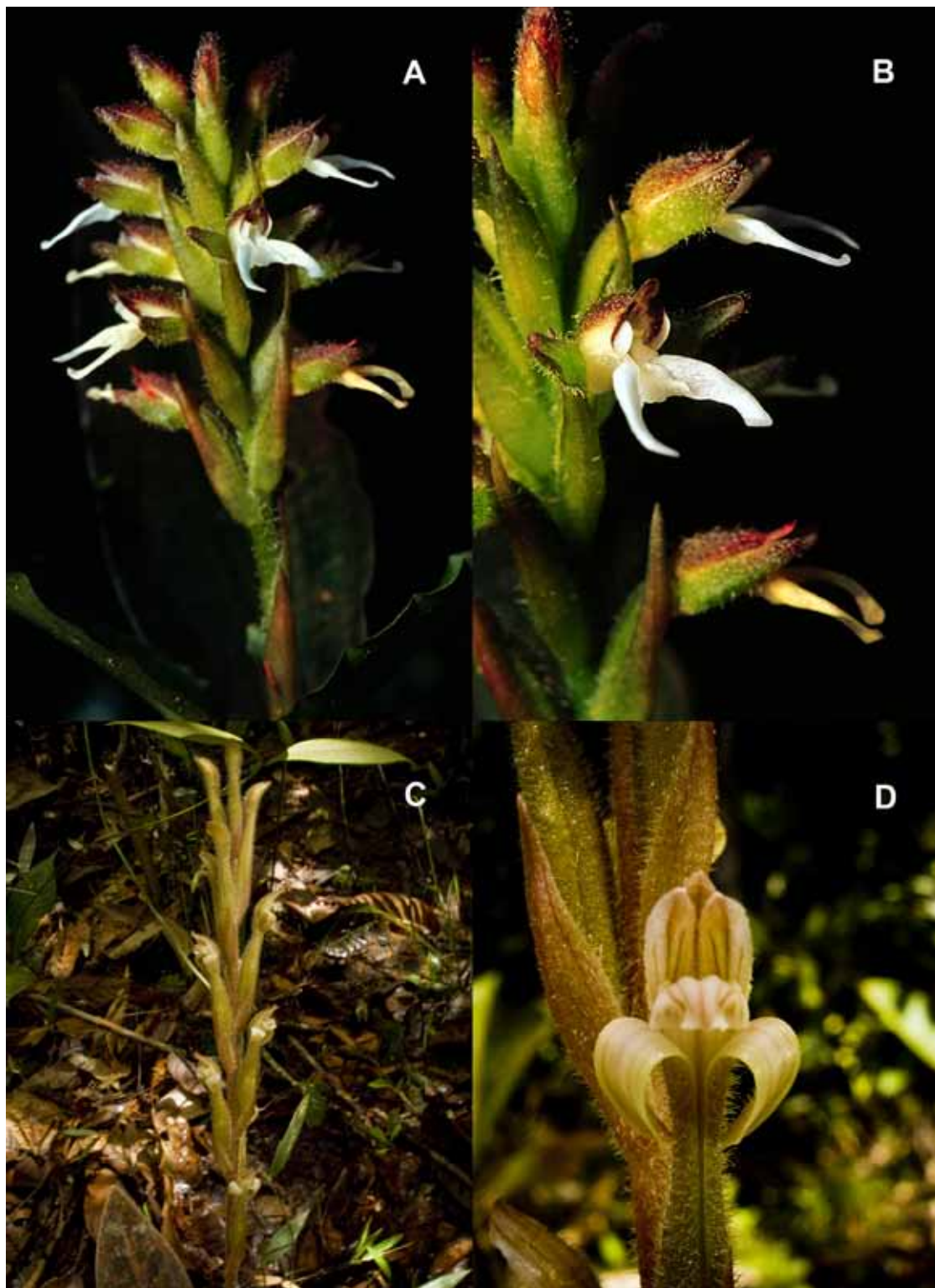
Subtribe Spiranthinae Lindl. (Garay, 1982; Salazar, 2003: 164; Salazar *et al.*, 2003).

Sarcoglottis Presl, Rel. Haenk. 1: 95, t. 15. 1827 (Garay, 1982; Salazar, 2003: 246).

Sarcoglottis maroaënsis G. A. Romero & Carnevali, *sp. nov.*

TYPE: VENEZUELA. Amazonas: Municipio Autónomo Maroa, carretera Yavita-Maroa, cerca del aeropuerto, 100 m, “hierba terrestre, raíces carnosas, hojas en el lado superior rojizas con manchas verde oscuro, en el lado inferior rojo-moradas con la nervadura principal

Right: FIGURE 1. A—B *Ligeophila gavilanensis* Ormerod & G. A. Romero. A. Inflorescence. B. Closeup of flowers. C—D. *Sarcoglottis maroaënsis* G. A. Romero & Carnevali. C. Inflorescence. D. Closeup of flowers. Photographs *in situ* by G. A. Romero-González. A—B based on Romero *et al.* 3066; C—D based on Romero *et al.* 3620.



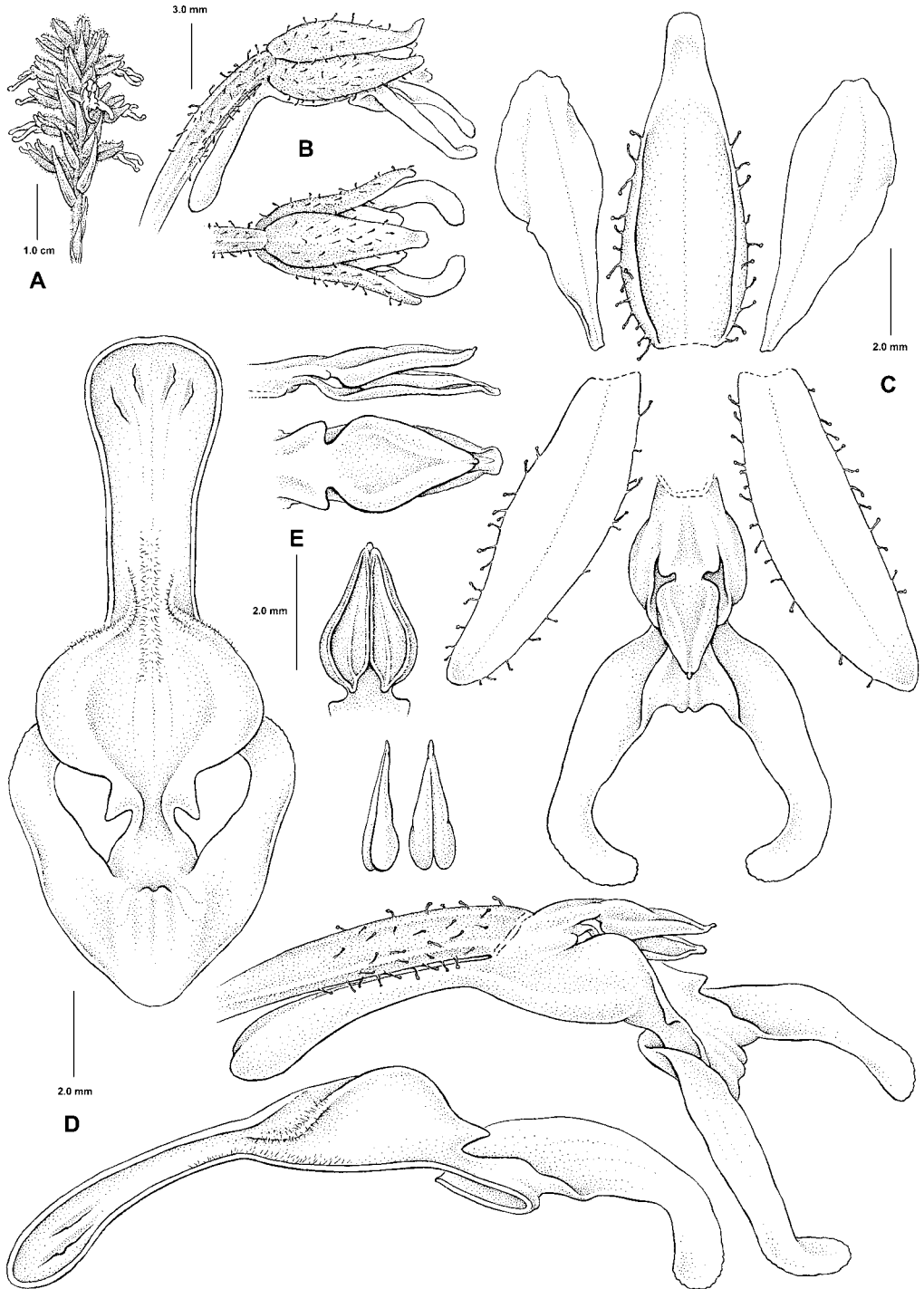


FIGURE 2. *Ligeophila gavilanensis* Ormerod & G. A. Romero. A. Inflorescence. B. Two views of the flower. C. Floral diagram. D. Three views of the labellum. E. Three views of the column and two views of the pollinarium. Drawn by Bobbi Angell based on the holotype.

roja, pedúnculo rosado, obscuro en la base, más pálido hacia el ápice, brácteas rojizas, sepalos verde pálido con nervios rojo pálido, pétalos y labelo crema con nervios rojo pálido”, 29 July 2006, *G. A. Romero, C. Gómez & G. Gerlach 3620* (Holotype: TFAV; Isotype: AMES). FIG. 1B–C, 3.

A *Sarcoglottis metallica* (Rolfe) Schltr. floribus rubentibus ac foliis item rubentibus et maioribus, a *Sarcoglottis ventricosa* (Vell.) Hoehne inflorescentia laxiore non lanuginosa, floribus minoribus necnon forma segmentorum floralium diversa.

Terrestrial *herbs*. *Roots* clustered, fleshy. *Leaves* 3–6, in a basal rosette, petiolate, dark brown above with dark green and lighter red spots, light reddish brown throughout below, with a prominent, reddish central nerve and two additional flat, reddish nerves on each side; petiole reddish, lighter toward the base, 3.0–5.0 cm, narrow, decurrent; blade up to 18.0 x 4.50 cm, elliptic lanceolate to oblanceolate, acute, attenuate. *Inflorescence* a 10-flowered raceme, multilateral. Peduncle 7.0 mm in diameter at the base and 5.0 mm in diameter below the rachis, erect, glandular; *bracts* reddish, 4, shorter than the internodes, acute, herbaceous, glandular. *Rachis* 14.0–15.0 cm, reddish, densely glandular. *Floral bracts* reddish, lighter toward the base, 15–18 mm long, lanceolate, acute, herbaceous, glandular throughout. *Flowers* erect. Pedicel 5.0 mm long, twisted. *Ovary* yellowish green, 25.0–39.0 mm long, glandular-pubescent throughout. *Dorsal sepal* 11.0–12.0 x 3.0–3.2 mm, oblong-lanceolate, acute, sparsely glandular-pubescent outside, 3-nerved. *Lateral sepals* yellowish green dorsally, light cream ventrally, fused with the ovary for 5.0–6.0 mm, free parts reflexed, 9.0–10.0 x 3.5–4.0 mm, oblanceolate-falcate, acute, sparsely glandular-pubescent outside, 5-nerved, the nerves dark brownish-red. *Petals* light cream, 10.0–11.0 x 2.5 mm, oblanceolate, acute, asymmetric, glandular along the outer margins, 3-nerved, the nerves dark brownish red. *Labellum* subsessile, thin, constricted near the apex (the constriction marking the separation between hypochile and epichile), light cream with dark brownish markings; hypochile 16.0–18.0 x 4.5–5.0 mm, cuneate in the densely glandular basal half, obovate above, with two fleshy, digitate retrorse

auricles at the base; epichile 3.0 x 5.0 mm, more or less transversely elliptic, crenate and plicate along the margins. A roughly V-shaped, rugose thickening starts near the apex of the epichile and extends into the distal part of the hypochile. *Column* cream, 6.0–7.0 mm long, erect; column foot adnate to the ovary. *Anther* 4.5–5.0 mm long and 3.0 mm wide. *Rostellum* remnant thickened at the margins, truncate. *Pollinarium* yellow, 4.5 mm long, viscidium whitish, 1.5 mm wide (description based on a fresh specimen and on flowers preserved in alcohol).

ETYMOLOGY: Named after the type locality, Maroa, the capital of the municipality.

ADDITIONAL SPECIMEN EXAMINED: VENEZUELA. Amazonas: municipio Autónomo Maroa, alrededores de Boca Chico, 100 m, 23 January 1998, “hierba terrestre, entre la hojarasca, hojas rojizas con manchas rojas más claras, sin flores, único individuo visto”, *G. A. Romero, C. Gómez & L. M. Campbell 3177* (TFAV); municipio Autónomo Atabapo, Cerro Yapacana, 1200 m, “flowers brown-green, leaves spotted with purple brown”, 3 January 1953, *B. Maguire, R. S. Cowan & J. J. Wurdack 30686* (NY).

DISTRIBUTION: Venezuela, Amazonas (endemic).

This plant previously had been detected along the Yavita-Maroa road several times but never with flowers. As such, it had been preliminarily identified as *Pelexia callifera* (C.Schweinf.) Garay, a species with which it shares many vegetative characters. However, an examination of the flowers of the type showed that the plant clearly was not referable to *Pelexia* Poit. ex Lindl. but to *Sarcoglottis* Presl (see keys and generic descriptions in Garay, 1980 and Salazar, 2003: 166–168, 232, 234, 247). Further comparison to the known species of *Sarcoglottis* showed that it was an undescribed species. In shape and size of labellum it is similar to *S. metallica* but the new species differs in the cream flowers with dark reddish veins in the sepals, petals, and labellum, and the leaves of different color. In flower color it is similar to *S. ventricosa* (Vell.) Hoehne (synonym: *S. rufescens* Klotzsch) but the inflorescence of *S. maroaënsis* is more lax and not lanate, the flowers are smaller, and lateral sepals and labellum are different.

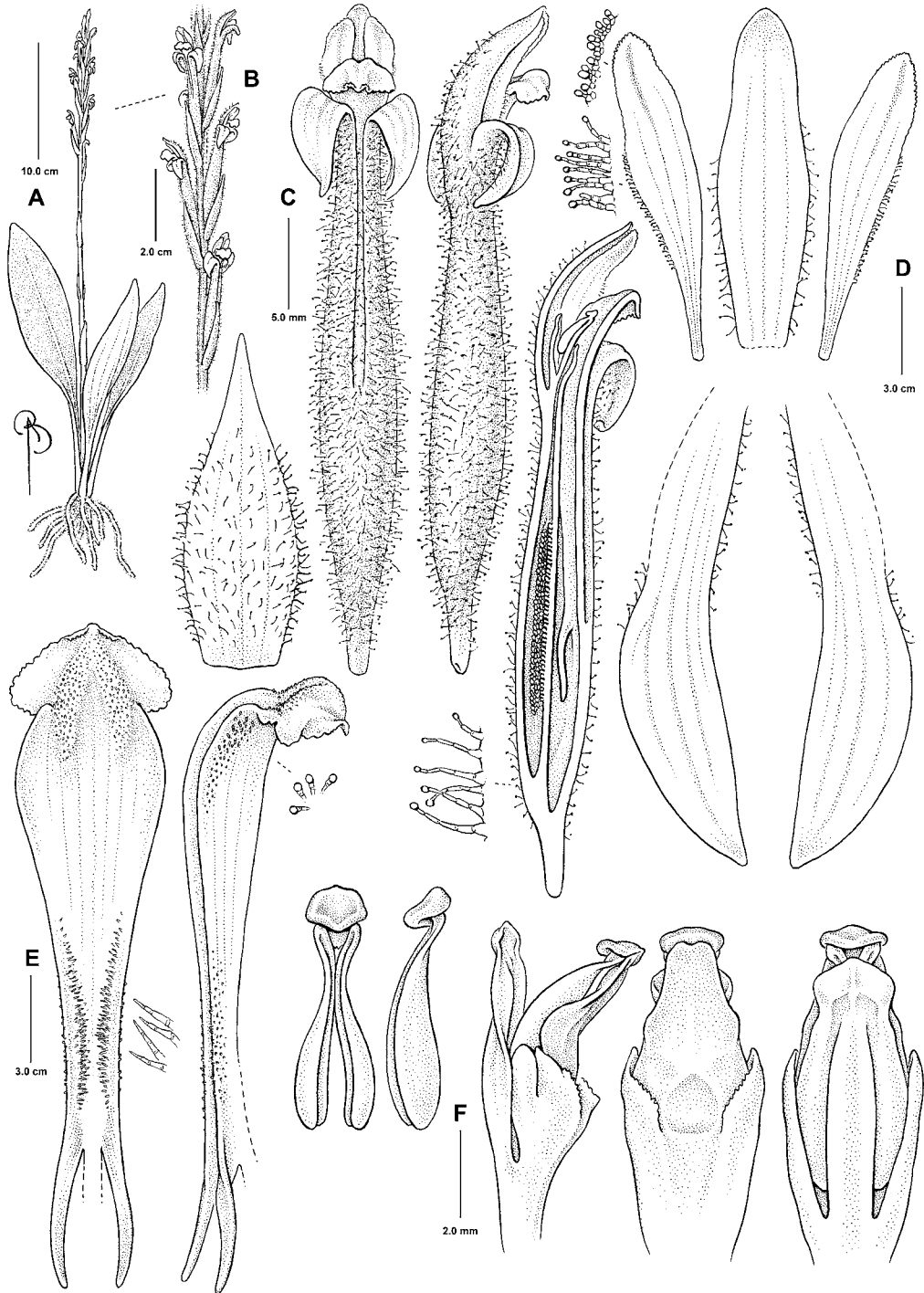


FIGURE 3. *Sarcoglottis maroaënsis* G. A. Romero & Carnevali. A. Plant. B. Inflorescence. C. Three views of the flower. D. Floral diagram. E. Two views of the labellum. F. Three views of the column and two views of the pollinarium. Drawn by Bobbi Angell based on the holotype.

Sarcoglottis stergiosii Carnevali & I. Ramírez, 3: 124, fig. 12. 1993 3: 124, fig. 12. 1993.

TYPE: VENEZUELA. Amazonas: municipio Autónomo Río Negro, selva pluvial, alrededores de San Carlos de Río Negro y camino que conduce a Solano, 23—29 July 1982, “hierba, flores blancas”, B. *Stergios* & G. *Aymard* 4400 (holotype: VEN; isotypes: NY, PORT, TFAV).

ADDITIONAL SPECIMEN EXAMINED: COLOMBIA. Amazonas: Río Apaporis, Cachivera de Jirijirimo y alrededores, 250 m, “Terrestrial, flowers white, leaves mottled grey-purple”, 16 September 1951, R. E. *Schultes* & I. *Cabrera* 14031 (AMES).

Here we report the isotype at NY that was not cited in the protologue, and extend the distribution of this species, previously thought to be endemic to Venezuela (Carnevali & Ramírez 2003), to the Colombian Amazon.

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A NEW SPECIES OF *LOPHIARIS* RAF. (ORCHIDACEAE) FROM THE PACIFIC COASTAL OF MEXICO

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ABSTRACT. A species of *Lophiaris* Raf. (Orchidaceae: Cymbidieae: Oncidiinae), *Lophiaris natalieae*, from Jalisco, Mexico, is proposed as new. The new species is described, illustrated and compared to *Lophiaris lurida*, from which is different by its lateral sepals shortly connate at base, and its transversely narrower central labellum lobe. Its distribution and habitat are discussed. Conservation status of the new taxon is assessed against the MER criteria.

RESUMEN. Una especie de *Lophiaris* Raf. (Orchidaceae: Cymbidieae: Oncidiinae), *Lophiaris natalieae*, de Jalisco, México, es propuesta como nueva. La nueva especie es descrita, ilustrada y comparada con *Lophiaris lurida*, la cual es diferente por sus sépalos laterales cortos y fusionados en la base, y con el lóbulo central del labelo transversalmente mas estrecho. Su distribución y hábitat son discutidos. El estado de conservación del nuevo taxon es analizado con base a los criterios del MER.

KEY WORDS: *Lophiaris*, MER, Mexico, Jalisco, Oncidiinae, Orchidaceae

During the course of a systematic and phylogenetic study of the genus *Lophiaris* Raf. (Balam *et al.*, in prep.), a hitherto unknown taxon with pale grayish green to light yellow flowers, spotted with dark red to light brown, was detected. It has been collected in Jalisco, Mexico. The presence of a new taxon of *Lophiaris* in this zone is surprising, since the area is close to some large cities and touristic developments. Only *L. oestlundiana* (L.O. Williams) Braem, with a differently shaped labellum and matte, brick-red flowers, was previously known from the area.

In accordance with phylogenetic studies of the *Trichocentrum* Poepp. & Endl. *s.l.* complex (for a discussion of generic limits within the *Trichocentrum* complex see Balam, 2007; Cetzal, 2007; see also discussion and literature citations in Jiménez-Machorro & Carnevali, 2001; Cetzal *et al.*, 2008; Carnevali *et al.*, 2009), we place the new species in the genus *Lophiaris*.

This new entity is probably endemic to the Cabo Corrientes area in NW Jalisco (Pacific Coastal Plain).

This area is notheworthy because of the presence of several species that are either endemic or otherwise mainly restricted there. These include, among the Orchidaceae, taxa such as *Lophiaris oestlundiana* (L.O. Williams) Braem, *Encyclia spatella* (Rchb. f.) Schltr., *E. trachycarpa* (Lindl.) Schltr., *Catasetum pendulum* Dodson, *Mormodes badia* Rolfe ex Watson and a few others, including an as yet undescribed species of *Cohniella* Pfitzer. There are also a few endemic Bromeliaceae such as *Tillandsia jalisco monticola* Matuda; *T. paucifolia* var. *schubertii* F. Ebel & J. Röth, and *Ursulaea tuitensis* (Magaña & E. J. Lott) Read & Baensch. The area of Cabo Corrientes is where the Neovolcanic Transversal Axis reaches the Pacific coast, creating barriers to the distribution of biotas from further south and north, while it apparently serves as a corridor for biotas along a west to east axis.

The novelty here proposed, *Lophiaris natalieae* Balam & Carnevali, is morphologically similar to *L. lurida* (Lindl.) Braem, which ranges from the Gulf Coastal Plain in Mexico to northeastern Venezuela. The

differences between these two species are discussed below.

Lophiaris natalieae Balam & Carnevali, *sp. nov.*

TYPE: México. Jalisco: Cabo Corrientes, 1.3 km después del puente Los Horcones, ca. 11 km después de Boca de Tomatlán, rumbo a El Tuito, 20°26'47"N 105°17'05"W, 460–470 m; floreciendo en cultivo en Dzityá, Yucatán, 25 Marzo 2008, de una planta colectada en Julio de 2007, *G. Carnevali* & *I. Ramírez 7271* (holotype, CICY; isotype, AMES). FIG. 1.

Species haec *Lophiaris luridae*, sed sepalis lateralibus liberis, callo 5-partito dentibus liberis (vs. 5 partitum, dentibus carina longitudinalis instructis) quam isthmo brevior (vs. subaequans vel longior), lobulo centrali 2.5–3 x latior quam longior (vs 1.5–2) differt.

Epiphytic herb, typical for the genus. *Pseudobulbs* clustered, subcylindrical, ca. 13.9 x 10.2 mm, dark or medium green, compressed. *Leaves* solitary, conduplicate, coarse, 23–24 cm long, ca. 2.4–3.2 cm wide at the base, 3.3–3.75 cm in the median portion, and 2.4–2.5 cm at apex, oblong-elliptic, acute, erect, margins erose-dentate, yellowish olive green or dark green, conspicuously spotted with dark red-brown. *Inflorescence* paniculate, erect-arching, ca. 33–155 cm long, originating from the base of the mature pseudobulb, one per pseudobulb. *Flowers* showy, resupinate, ca. 20.3–24.7 mm in diameter, the labellum brown-greenish (chocolate), or mustard yellow apically, with a matte texture, basal lobes and isthmus shiny bright red or orange, callus bright red and yellow or light and dark orange with rose-pink, shiny; the bases of the sepals and petals pale grayish green or light yellow, spotted or mottled with dark red or light brown; *dorsal sepal* clawed, blade rounded-obtuse or rounded-acute, undulate, 5.2–6.6 x 4.0–7.2 mm, claw 2.5–3.9 x 1.0–1.7 mm; *lateral sepals* clawed, shortly connate at base, blade ovate-acute or obovate, 4.7–6.2 x 3.2–4.9 mm, claw 3.0–4.5 x 1.2–1.8 mm; *petals* frilled, undulate, swept forward at the apices, blade ovate-oblong, basal portion abruptly narrowed 5.8–6.8 x 5.2–7.1 mm, claw 2.2–2.9 x 2.0–2.8; *labellum* 9.5–11.8 mm diameter, 3-lobed, pandurate, forming a 135° angle to the column; the lateral lobes 6–8 x 1.5–2.5 mm, upper and lower margins reflexed-rounded,

subtriangular or subcuadrado when spread; central lobe broadly reniform, 5.5–6.4 x 11.2–13.8 mm, transversely narrower, shallowly retuse with a minute apiculus; isthmus 1.0–1.5 x 2.4–3.8 mm, short and narrow; callus 3.2–4.5 x 2.6–4.4 mm, made up of 5 truncate independent units: two basal units composed of 5–6 teeth, a small pair of porrect teeth at the base of the basal lobes, two lower units which are apically rounded, and a central keel linking the three teeth but not reaching the proximal section of the basal pairs of units. *Column* 3.4–5.6 x 1.9–3.8 mm, thick and stout dorso-ventrally, luminous white, sometimes touched with pink; the infrastigmatic tabula prominent, subquadrado, yellow, with red-orange blotches; column wings 2.6–3.3 mm long, dolabriform, the posterior lobe 1.2–2.7 mm wide, white or pale pink, elongate; stigmatic cavity subquadrado, bright white. *Anther* 1.3–4.0 x 2.2–2.9 mm, ovoid, extended into a deep, internally rimmed, visor-like extension at the ventral base, white or yellow-cream, with a thick external keel at the medial portion. *Pollinarium* 2.9–3.2 mm long, composed of two obovate-elliptic pollinia, 1.7–2.1 x 1.0–1.6 mm; stipe short, laminar, translucent white, deeply concave with a flaring; viscidium horse shoe-shaped. *Capsule* unknown.

This description was compiled with the use of the herbarium specimens, as well as measurements taken from live or pickled material belonging to the original population.

PARATYPES: México. **Jalisco:** Cabo Corrientes, camino El Tuito-La Chacala, a 4 km de El Tuito, Selva mediana subperennifolia en buen estado de conservación, 20°20'14" N 105°21'09"W, 586 m, floreciendo en cultivo en Mérida, Yucatán, 13 Marzo 2008, de una planta colectada el 28 de Julio de 2007 (flowers preserved in spirit), *R. Balam 104* (CICY); Puerto Vallarta, south of Puerto Vallarta, dry, open forest on top of a hilltop, 400 m, 21 Julio 1987 (flowers preserved in spirit), *Warford & Amezcua s.n.* sub. *G. Carnevali 6043* (CICY); Tomatlán, 13.5 km después de Horquetas de Caimán, a 9 km después de la desviación a Tomatlán rumbo a Barra de Navidad, 19°42'43"N, 105°17'54"W, 125 m, floreciendo en cultivo en Dzityá, Mérida, Yucatán, 15 Abril 2007, de una planta colectada el 30 Julio de 2003, *G. Carnevali* & *I. Ramírez 6931* (CICY).

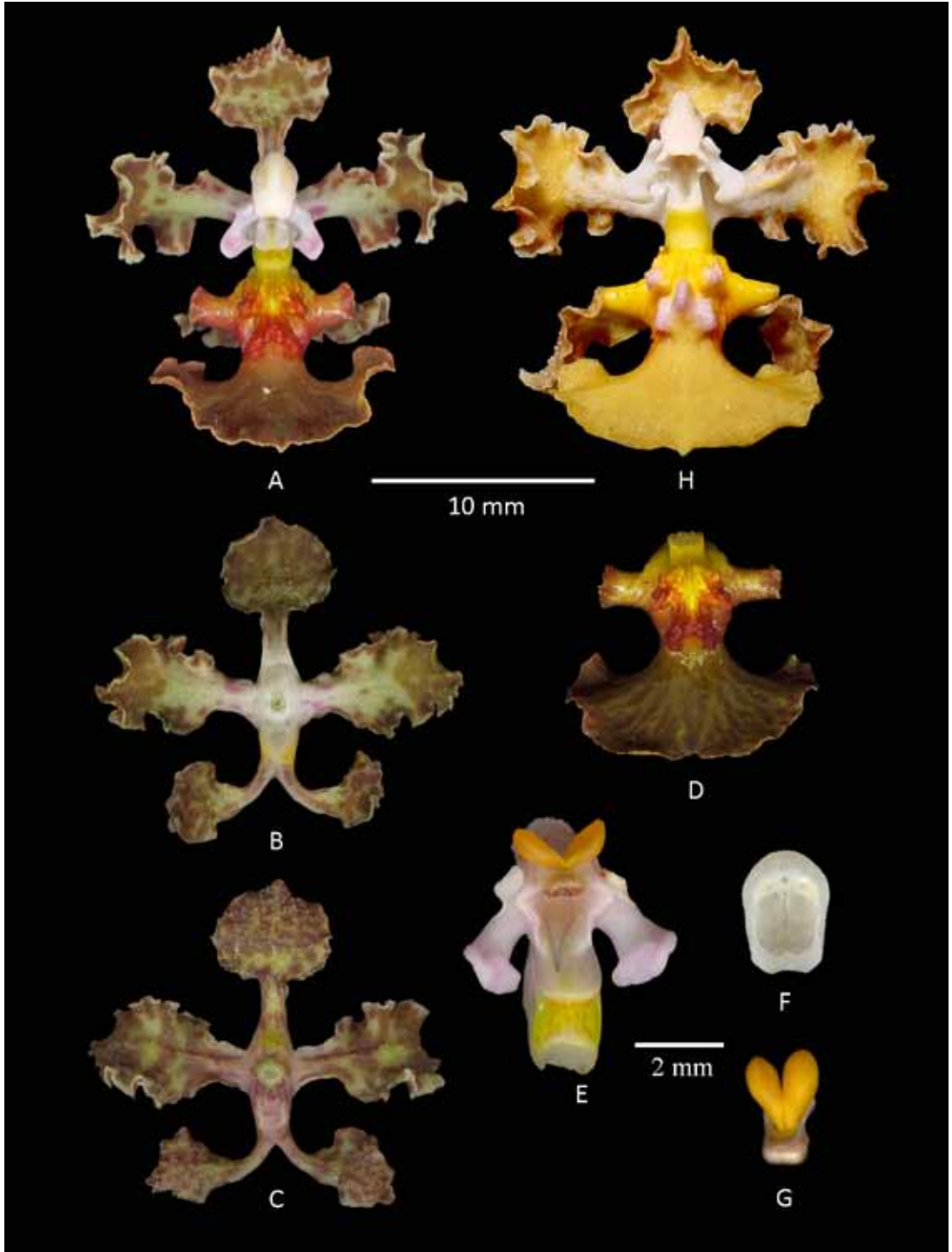


FIGURE 1. *Lophiaris natalieae*. A-H. Flower. B-C. Sepals and petals, front and back view. D. Labellum. E. Column. F. Anther cap. G. Pollinarium. A—G. Based on *R. Balam 104* (CICY). H. Based on *G. Carnevali & I. Ramirez 6931*(CICY). Scale: A-D, H. 10 mm; E-G. 2 mm. Assembled by W. Cetzal Ix.

EPONYMY: Dedicated to Natalie Warford, a former resident of Puerto Vallarta, Jalisco, who was the first to recognize the existence of this species as an entity distinct from other *Lophiaris* species from western Mexico. She cultivated plants and eventually prepared vouchers of this new species, which she also drew beautifully.

Lophiaris natalieae is phenetically similar and apparently phylogenetically related to *L. lurida*. This last species is restricted to the Gulf drainage in Mexico, extending southwards into Central America and coastal Colombia and Venezuela. *Lophiaris natalieae* is distinguished from *L. lurida* by its lateral sepals that are fused on the lower $\frac{1}{4}$, while they are free in *L. lurida*. Furthermore, the central lobe of *L. natalieae* is transversely narrower than that of *L. lurida*, 2.5-3 times broader than its length in *L. natalieae* while this same structure is 1.5-2 times broader than long in *L. lurida*. The calli of both species are also different. In *L. natalieae* the callus is made up of five independent units. These units are variable in shape (rounded to acute) and color (pink to red or yellow), but are always free from each other. On the other hand, *L. lurida* presents all the structures of the callus associated to a platform over which there are two rows of calli, distal and proximal; these two rows are linked by a medial, longitudinal keel that protrudes beyond the two teeth of the distal row. The distal row of callus in *L. lurida* reaches (or almost) the base of the central labellum lobe, while the distal row of callus in *L. natalieae* is placed on the disk and never reaches the isthmus and the base of the central lobe. Another distinction is the size of the flowers; the flower of *L. natalieae* is much smaller (24 mm vs. 30 mm in *L. lurida*).

DISTRIBUTION AND HABITAT: *Lophiaris natalieae* seems to be restricted to the western extreme of the Neovolcanic Transversal Axis on the Pacific coast in Jalisco, and to sea facing-slopes along the Pacific Coast of the Sierra Madre Occidental in Nayarit. The known distribution of this species is disjunct, consisting of three sites in Jalisco (Pacific Coastal Plain): one at Cabo Corrientes (southwest of El Tuito) (*R. Balam 104*), other at Tomatlán (*G. Carnevali & I. Ramírez 6931*) and we have had the opportunity of dissecting a flower preserved in spirit from a

plant collected south of Puerto Vallarta (*Warford & Amezcua s.n. sub. G. Carnevali 6043*). The species has been collected mostly at elevations ranging from 400–600 m in low caducifolious forest to medium-statured subcaducifolious forest.

MER RISK CRITERIA. We determined risk status of this new species through the Método de Evaluación del Riesgo de Extinción de las Especies Silvestres en México (Method for the Evaluation of Risk of Extinction for Mexican Wild Species: MER; SEMARNAT 2002) because it has been required by Mexican law since 2002 for listing organisms for protection. This method would provide a reasonably reliable way to identify species of conservation concern and can meet its intended goals of facilitating timely conservation decisions and generating testable hypotheses in future studies. MER methodology consists of four risk criteria, divided into risk categories with numerical scores, with higher numbers denoting higher risk (Tambutti et al. 2001). The total score is calculated by summing the results from its four criteria, establishing a numerical value with which the category of risk of the species is determined: between 12 and 14 are considered in danger of extinction (P); those with a score of 10 or 11 are threatened (A), and those of 9 or below are considered to be of little current risk (Pr) (SEMARNAT 2002). *Lophiaris natalieae* is known from three isolated localities restricted, where it is uncommon and at low population densities, obtaining total assessment 12 scores. This suggested that it might be best considered danger of extinction (Pr) according to MER criteria (SEMARNAT 2002).

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A LA TERCERA SE GANA: THE VALIDATION OF *BENZINGIA* (ORCHIDACEAE: ZYGOPETALINAE)

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ABSTRACT. When *Benzingia* was first proposed in 1989, the protologue included two species (*Benzingia hirtzii* sp. nov. and *B. estradae* comb. nov.), which required two separate Latin descriptions or diagnoses (generic and specific) for *Benzingia* and *B. hirtzii*. The author, however, provided only a *descriptio generico-specifica*. Therefore, the generic name, the new species, and the proposed combination were not validly published. An attempt to validate the genus and the two species was made by Dodson and Romero in 1995, but it also failed because it did not include separate Latin descriptions for the genus and the proposed type species. Seven species names referred to *Benzingia* in the meantime are also invalid. All the ten relevant names are here validated (the generic name, the new species, and eight new combinations).

RESUMEN. Cuando se propuso *Benzingia* por primera vez en 1989, el protólogo incluía dos especies (*Benzingia hirtzii* sp. nov. y *B. estradae* comb. nov.), lo que requería descripciones o diagnósicos en latín separadas para el género y para la especie nueva. Sin embargo, el autor sólo publicó una *descriptio generico-specifica*. Por consiguiente, *Benzingia*, la especie nueva y la nueva combinación no fueron publicadas válidamente. Se trató de validar el género en 1995, pero el esfuerzo falló porque no se incluyeron las descripciones separadas en latín del género y de la especie tipo. Mientras tanto, los nombres de las siete especies adicionales que hasta el momento se han referido a *Benzingia* también son inválidos. Aquí se validan los diez nombres relevantes (el nombre genérico, la especie nueva y ocho nuevas combinaciones).

KEY WORDS: *Benzingia*, Orchidaceae, validation, Zygopetalinae

Introduction. The genus *Benzingia* Dodson was first proposed in 1989. A *descriptio generico-specifica* was provided for the generic name and for a new species, *B. hirtzii* Dodson. In the protologue, however, Dodson (1989) also proposed a new combination, transferred from *Chondrorhyncha* Lindl. According to article 42.1 of the International Code of Botanical Nomenclature (McNeill et al., 2006), *Benzingia*, the new species, and the proposed combination were not validly published (see Art. 42.1, Ex. 1), because two separate Latin descriptions or diagnoses were required for the generic name and the new species.

Dodson and Romero (1995) attempted to validate the genus but failed to provide the required separate Latin descriptions for the genus and the type species: the names included therein were again not validly published. In the meantime, seven additional new combinations have been proposed in *Benzingia*

(Dressler in Whitten *et al.*, 2005; Harding, 2008: 32). Since the generic name had not been validly published, however, these names are considered invalid.

Benzingia and *B. hirtzii* are validly described here, for which we provide separate Latin diagnoses, and eight relevant names at the rank of species are validated. In personal communications, both R. L. Dressler and P. A. Harding consented to have their new combinations republished here.

***Benzingia* Dodson, gen. nov.**

Synonyms: *Ackermania* Dodson & R. Escobar, *Orquideología* 18: 202. 1993, non *Ackermania* Pat. (1902).

Benzingia Dodson, *Icon. Pl. Trop. Ser. 2, 5: t. 406. 1989, nom. invalid.*

Benzingia Dodson, *Lindleyana* 10: 74. 1995, *nom. invalid.*

TYPE: *Benzingia hirtzii* Dodson

Habitus *Steniae* Lindl. similis sed labello spatulato non profunde saccato, et habitus *Chondrorhynchae* Lindl. similis sed sepalis patentibus nec retrorsis neque falcatis distinguitur.

Benzingia caudata (Ackerman) Dressler, *comb. nov.*

Basionym: *Chondrorhyncha caudata* Ackerman, Selbyana 5: 299. 1981.

Synonym: *Benzingia caudata* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia cornuta (Garay) Dressler, *comb. nov.*

Basionym: *Chondrorhyncha cornuta* Garay Orquideologia 5: 20. 1970.

Synonym: *Benzingia cornuta* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia estradae (Dodson) Dodson, *comb. nov.*

Basionym: *Chondrorhyncha estradae* Dodson, Icon. Pl. Trop. t. 22 (as “*Chondroryncha*”). 1980.

Synonym: *Benzingia estradae* Dodson, Lindleyana 10: 74. 1995, *nom. invalid.*

Benzingia hajekii (D.E.Benn. & Christenson) Dressler, *comb. nov.*

Basionym: *Ackermania hajekii* D.E.Benn. & Christenson, Icon. Orchid. Peruvianum t. 602. 2001.

Synonym: *Benzingia hajekii* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia hirtzii Dodson, *sp. nov.*

TYPE: ECUADOR. Imbabura: Santa Rosa de Chaco, 8 km East North of Lita on road Ibarra to Lita, 1150 m, 19 January 1987, C. H. Dodson, A. Hirtz, D. Benzing & C. A. Luer 16893 (holotype, MO; isotypes, QCNE, K, SEL).

Synonym: *Benzingia hirtzii* Dodson, Icon. Pl. Trop. Ser. 2, 5: t. 406. 1989, *nom. invalid.*

Benzingia hirtzii Dodson, Lindleyana 10: 74. 1995, *nom. invalid.*

Species haec *Benzingiae estradae* (Dodson) Dodson similis, sed inflorescentia erecta, labello basi leviter concavo apice rotundo et ovario geniculato distinguitur.

Epiphyte. Plant to 15 cm tall. Rhizome short, stems

erect, very short, without pseudobulbs, surrounded by imbricating, distichous leaf-bearing sheaths. Leaves elliptic-oblong, acuminate at the apex, narrowing to the base and the articulated junction with the sheath, membranaceous, to 12 x 1.6 cm. Inflorescence 1-flowered, erect, usually one inflorescence produced from each leaf sheath. Floral bracts triangular, 3 mm long. Ovary geniculate so that flower is nonresupinate, to 2 cm long, terete. Flower yellow, the sepals and petals spotted with red-brown, the lip yellow with an orange callus, abundantly spotted with red-brown. Sepals spreading, free; dorsal sepal oblong-ovate, 1.7 x 0.5 cm; lateral sepals obliquely oblong-ovate, 1.8 x 0.5 cm. Petals oblong-ovate, spreading, obtuse, 1.7 x 0.5 cm. Lip shallowly concave, scoop-shaped, rotund, not surrounding the column, 2.2 x 2.2 cm, united to the column foot at the base, with a flat callus down the midline. Column arcuate, subterete, slightly winged on each side below the stigma, 1.5 cm long, produced into a terete foot 0.8 cm long. Pollinia in 2 unequal pairs attached to a rectangular stipe, the latter attached to a cordiform viscidium.

Benzingia jarae (D.E.Benn. & Christenson) Dressler, *comb. nov.*

Basionym: *Ackermania jarae* D.E.Benn. & Christenson, Brittonia 47: 182. 1995.

Synonym: *Benzingia jarae* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia palorae (Dodson & Hirtz) Dressler, *comb. nov.*

Basionym: *Stenia palorae* Dodson & Hirtz, Icon. Pl. Trop. ser. 2, 6: t. 583. 1989.

Synonym: *Benzingia palorae* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia reichenbachiana (Schltr.) Dressler, *comb. nov.*

Basionym: *Chondrorhyncha reichenbachiana* Schltr., Repert. Spec. Nov. Regni Veg. 17: 15. 1921.

Synonym: *Benzingia reichenbachiana* Dressler, Lankesteriana 5: 93. 2005, *nom. invalid.*

Benzingia thienii (Dodson) P.A.Harding, *comb. nov.*

Basionym: *Cochleanthes thienii* Dodson Icon. Pl. Trop. t. 26. 1980.

Synonyms: *Chondrorhyncha thienii* (Dodson)

Dodson Selbyana 7: 354. 1984.
Benzingia thienii P.A.Harding, Huntleyas 32.
2008, *nom. invalid.*

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***EPIDENDRUM JALCAËNSE* (ORCHIDACEAE), A NEW SPECIES FROM NORTHERN PERU**

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ABSTRACT. *Epidendrum jalcaëense* (Orchidaceae: Laeliinae), a new species from Northern Peru is described and illustrated.

RESUMEN. Se describe e ilustra una nueva especie para la ciencia perteneciente al género *Epidendrum jalcaëense* (Orchidaceae: Laeliinae), proveniente del Norte del Perú.

KEY WORDS: Orchidaceae, *Epidendrum*, Jalca, Peru

The orchid family is the most diverse group of flowering plants on our planet, with the genus *Epidendrum* being one of the most prolific with at least 1500 recognized species (Hågsater & Soto, 2005), distributed from North Carolina in the United States, to Argentina (Schweinfurth 1959).

Until 2003, no less than 2034 orchid species were reported from Peru (Brako & Zarucchi 1993, Ulloa et al. 2004) but this number is still growing as new species and records continue to appear.

In this article we describe and illustrate a new *Epidendrum* species recently discovered in Northern Peru.

Epidendrum jalcaëense Chocce, Dalström, Hågsater & Arnaiz, *sp. nov.*

TYPE: Peru: Lambayeque: Cañaris, 3401 m, 14 September 2007, *M. Chocce, J. Arnaiz and P. Rinza 2865*. (Holotype USM, illustration voucher). Fig. 1, 2.

A *Epidendro aristoloides* Hågsater & Dodson similis, sed foliis anguste ellipticis, flore aurantiaco niteniti, et labello 5 ad 7 carinato differt.

Plant epiphytic, erect, sympodial, 44-56 cm tall. *Roots* basal, fleshy, white, 1.5-2 mm thick. *Stem* simple, cane-like, terete, thin, straight, 40.5-51 x 0.54-0.6 cm. *Leaves* to 9, alternate, from the middle part of the stem toward the apex, articulated; sheaths tubular, grooved, smooth, 2-4.3 x 1.4-1.6 cm; blade narrowly elliptical, coriaceous, green, margin crenate, 4.7-6.6 x 1-1.5 cm, apex mucronate. *Spathaceous bract* not present. *Inflorescence* apical, racemose, arching, densely many-flowered, 12 cm long; peduncle short, terete, thin, arching, 4 cm long; rachis thin, terete, straight. *Floral bracts* shorter than the ovary, lanceolate, 4-5 x 1-1.5 mm. *Ovary* 18 mm long. *Flowers* to 9, simultaneous, resupinate, glossy orange, without fragrance. *Sepals* free, oblanceolate, fleshy, margin entire, 15.5-16.5 x 6-7 mm; lateral sepals aristate, with a dorsal keel; *petals* free, ovate, apex obtuse, 6-veined, margin entire, 15 x 10 mm; *lip* united to the column, 3 lobed, basally cordate, deeply notched, margin erose, 13.5 x 17 mm; basally ecallose, but with 5-7 prominent keels on the disc; lateral lobes reniform, somewhat larger than the midlobe, 6.5 x 8.5 mm; midlobe transversally oblong, apex broadly emarginate and diminutively

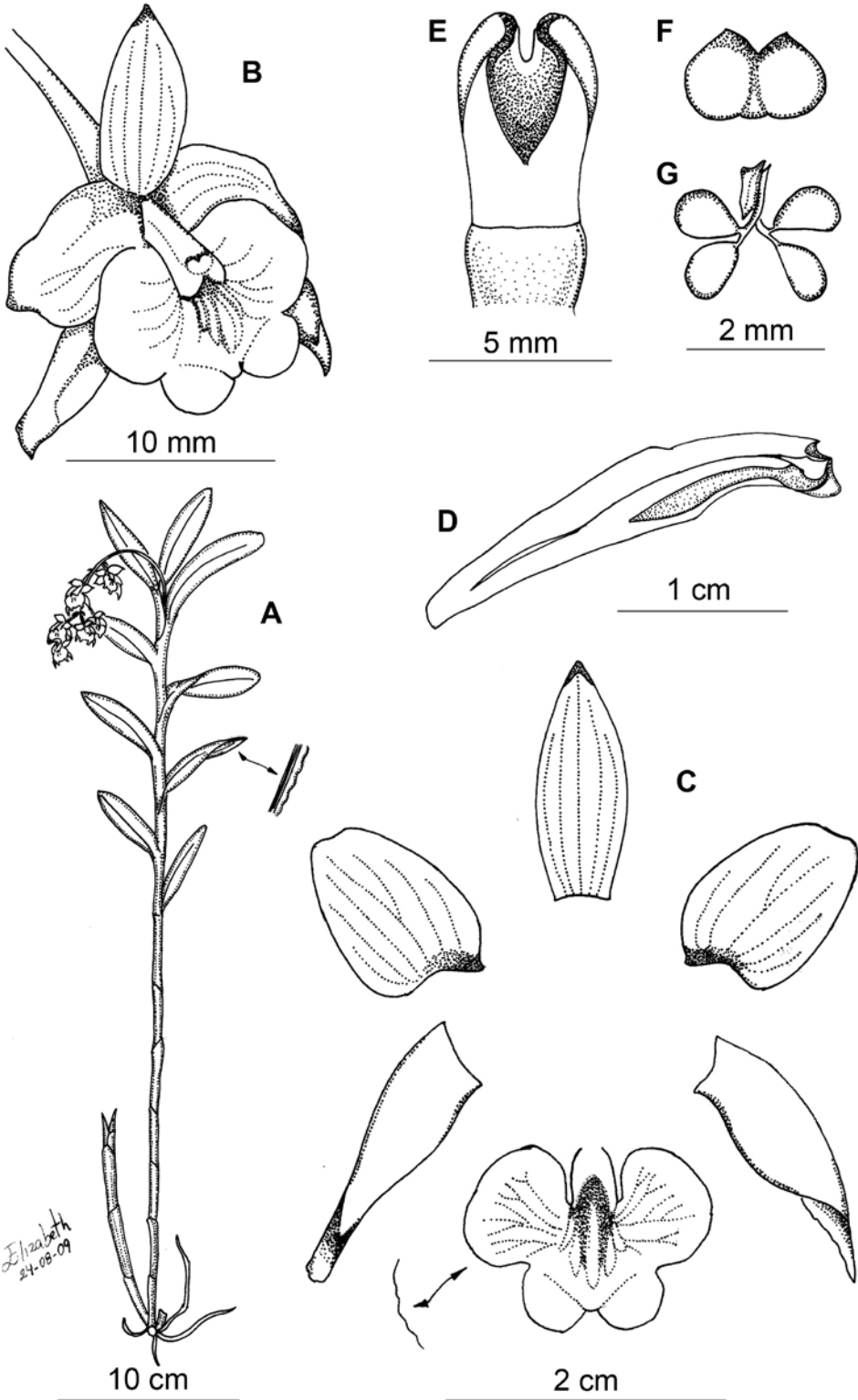




FIGURE 2. *Epidendrum jalcaëense*. Flowers (M. Chocce et al. 2865).

apiculate, forming a couple of semi rounded lobes, 5.3 x 11 mm. Column stout and thick, straight, apex slightly obconical, 10 mm long; clinandrium short with an entire margin; rostellum apical, fissured; nectary penetrating less ½ of the ovary, thick, smooth. Anther cap reniform, 4-celled. Pollinia 4, obovoid, laterally compressed;

POLLINATION: Presumed bird pollinated due to the floral characteristics that fit this pollination syndrome (Dressler 1982), and hummingbirds are abundant in the area where this showy orchid occurs.

ETYMOLOGY: The specific epithet refers to the term “Jalca” which is the name local people use for the ecosystem where *Epidendrum jalcaëense* occurs. Scientist, however, do not agree on the definition of the term “Jalca”. By compiling local references about the usage of “Jalca” in three northern regions (Lambayeque, Cajamarca y Amazonas) we can define “Jalca” as the “mosaic” of scrublands, grasslands

and forest fragments (patchily distributed) that begins right after the continuous forests border around 3000m elevation, and at lower elevation for the eastern zones in the Amazonas region.

Epidendrum jalcaëense is similar to *E. aristoloides* Hágsater & Dodson but with narrowly elliptic leaves, and with larger and glossy orange flowers, which make the inflorescences easily visible from a distance as they reach above the canopies of the gnarled and mossy trees where this orchid grows (Fig. 2).

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Left, FIGURE 1. *Epidendrum jalcaëense* Chocce, Dalström, Hágsater & Arnaiz. A — Habit. B — Flower. C — Dissected perianth. D — Ovary and column, longitudinal section. E — Column, ventral view. F — Anther cap. G — Pollinarium. Drawn by Margoth Acuña-Tarazona from the holotype.

ANÁLISIS DE LA SELECCIÓN DE SUSTRATO POR PARTE DE *DENDROPHYLAX LINDENII* (ORCHIDACEAE) EN CABO SAN ANTONIO, PENÍNSULA DE GUANAHACABIBES, PINAR DEL RÍO, CUBA

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RESUMEN. Se evalúa la preferencia de selección de sustrato por *Dendrophylax lindenii*, especie de orquídea epífita presente en Cabo San Antonio, Península de Guanahacabibes, Cuba. Se realizó un muestreo de todos los individuos de *D. lindenii* en dos transectos de 1000 m cada uno y ancho variable de acuerdo a la topografía del terreno. *D. lindenii* se encuentra sobre 19 especies diferentes de forofitos. Las especies más frecuentes fueron *Comocladia dentata*, *Diospyros crassinervis* y *Cedrela odorata*. Se localizaron un total de 344 individuos de *D. lindenii*, el 54,4% de los mismos se encuentran sobre *Comocladia dentata* (24,4%), *Sideroxylon foetidissimum* (10,8%), *Diospyros crassinervis* (9,9%) y *Tabebuia angustata* (9,3%). No se encontró preferencia por la altura o el DBH de las especies de árboles que ocupa. Las estrategias de conservación de *D. lindenii* deberían incluir la protección de las especies de árboles donde predomina esta especie de orquídea, en particular las dos especies con valor económico *D. crassinervis* y *C. odorata*.

ABSTRACT. In this study we analysed the host-tree preference by the epiphytic orchid *Dendrophylax lindenii* in Cabo San Antonio, Península de Guanahacabibes, Cuba. We surveyed two transects of 1000 metres and variable width, according to the topography. We noted the presence of the orchids and number counted all the individuals as well as the DBH at the insertion point of this orchid on the phorophytes and the height of trees in the semi-deciduous forest. We recording 344 individuals on 19 species of host tree (phorophyte). *D. lindenii* shows generalist behaviour on habitat selection, diameter and height insertion on host trees. The orchid was mainly found on *Comocladia dentata*, *Diospyros crassinervis* y *Cedrela odorata*. More than 54,4% of the *D. lindenii* were found on *Comocladia dentata* (24,4%), *Sideroxylon foetidissimum* (10,8%), *Diospyros crassinervis* (9,9%) y *Tabebuia angustata* (9,3%). Conservation effort should include the conservation of trees that are most frequently phorophyte of the orchid, especially the two species of trees which have commercial value, *D. crassinervis* y *C. odorata*.

PALABRAS CLAVES / KEY WORDS: especificidad de sustrato, epifitas, *Dendrophylax lindenii*, Orchidaceae, Cuba

INTRODUCCIÓN

Las orquídeas epifitas difieren en un importante número de aspectos de las orquídeas terrestres (Zotz & Schmidt, 2006). Por ejemplo, en las epifitas no existe una fase bajo tierra, y sus bajas densidades sugieren bajos niveles de competencia intra e interespecífica (Zotz & Hietz, 2001). El propio hábito epífita o litofítico de la mayoría de las especies de orquídeas las predispone a mantener una distribución en parches o agregada (Ackerman, 1995; Tremblay, 1997). Además, la dinámica de los sustratos (a nivel

de corteza, ramas, troncos y especies de forofitos) ejerce una influencia muy fuerte en la dinámica de las poblaciones de epifitas (Zotz & Schmidt, 2006).

Aunque las epifitas son un componente significativo en la diversidad vegetal, se conoce relativamente poco sobre la especificidad de la relación entre ellas y sus hospederos. Esta asociación adquiere particular interés si tenemos en cuenta que las mismas usualmente conviven en parches o mantienen una distribución discontinua (Trapnell & Hamrick, 2006).

La edad y el área disponible para la colonización pueden afectar la abundancia de epífitas y la composición de sus comunidades (Catling *et al.*, 1986; Pérez, 1982). Además, la arquitectura de los forofitos, como la estructura de su cobertura, ramificación, tamaño de las hojas, etc., pueden ejercer una fuerte influencia en la germinación y establecimiento de epífitas (Benzing, 1979) además de sus características químicas. Desde que se conoce que la disponibilidad de sitios tiene una fuerte influencia en la distribución de las poblaciones, es de suma importancia que las especies de forofitos sean consideradas en el desarrollo de estrategias de conservación de orquídeas (Migenis & Ackerman, 1993). Máxime cuando los “sitios” disponibles para las orquídeas epífitas son escasos y frecuentemente distribuidos de forma heterogénea con fuerte agregación de individuos (Ackerman, 1986).

En la península de Guanahacabibes conviven alrededor de 30 especies diferentes de orquídeas (Ferro *et al.*, 1995), ocupando, por tanto, casi todas las formaciones vegetales presentes en ese territorio. Sin embargo, la diversidad de especies arbóreas hace que la mayoría de ellas ocupe hábitats bien definidos. En el presente estudio se analiza la selección de sustrato por parte de *Dendrophyllax lindenbergii* para establecer si existe una especificidad orquídea-sustrato o solo una preferencia por determinadas especies de forofitos. Al mismo tiempo se analiza la preferencia que manifiesta esta especie de orquídea por los espacios que ocupa sobre los forofitos, específicamente altura y diámetro de los sustratos ocupados.

MATERIALES Y MÉTODOS

Dendrophyllax lindenbergii (D.I.) es una especie epífita áfila conocida como la orquídea “fantasma” u orquídea “rana”. Sus flores son grandes y vistosas con un excelente aroma lo que le confiere un lugar importante en las colecciones privadas. Esta especie está presente solo en Cuba y La Florida (U.S.A.). En la isla se le encuentra en zonas montañosas de la provincia Granma y Guantánamo, oriente del país, y se cita para zonas del norte de la provincia de Camagüey, reportes aún no comprobados. La población ubicada en Cabo San Antonio, es la única reportada para el occidente del país.

En el Cabo San Antonio se le encuentra en el bosque semidecíduo, a ambos lados del sendero El Catauro (Lat: N 21 52 172; Long: W 84 55 389), y en una profundidad en el bosque que no supera los 1000 m (Mújica, *inédito*). En el bosque semidecíduo de Cabo San Antonio las especies arbóreas más comunes son *Erythroxylum areolatum*, *Atheramnium lucidum*, *Sideroxylon foetidissimum*, *Cedrela odorata*, *Comocladia dentata*, y *Stigmatophyllum sagraeanum*. El suelo está conformado por carso desnudo, conocido como “diente de perro”, nombre que refleja lo accidentado del terreno (Acevedo, 1992).

Para el estudio de la comunidad de forofitos y selección de sustrato por parte de D.I. se trazaron dos transectos de 1 km de longitud cada uno y ancho variable (5-8 m) de acuerdo al relieve y la propia estructura que presenta la vegetación en esta zona. En ellos se procedió al marcaje con etiquetas de aluminio y numeración de todos los individuos de aquellas especies arbóreas que resultaron ocupados al menos una vez, estableciéndose la especie, altura y DBH de los mismos. De igual manera se marcaron y contabilizaron todos los individuos de D.I. presentes en los sustratos ocupados.

Para analizar las alturas y diámetros basales (DBH) de las especies arbóreas ocupadas y la distribución de las orquídeas en los forofitos hemos usado boxplots (box-and-whisker diagram) pues permite una adecuada representación gráfica de los datos de la distribución a través del primer cuartil $LQ(x_{.25})$, la mediana $LQ(x_{.50})$ y el tercer cuartil $LQ(x_{.75})$. Cualquier dato menor que $1.5 \cdot IQR$ (distancia intercuartil) en relación al primer cuartil ó mayor que $1.5 \cdot IQR$ en relación al tercer intercuartil, se considera un outlier. Los boxplots son especialmente útiles para comparar poblaciones o muestras pues no hacen ninguna asunción de la distribución estadística pues son no paramétricos (Tukey, 1977). Para las comparaciones entre estas distribuciones hemos usado el test no-paramétrico de Kruskal Wallis pues los datos no eran normales ni tenían homogeneidad de varianzas (Sokal & Rohlf, 1995). Para comprobar si existe una especificidad entre las especies de forofitos y la presencia de D.I. hemos aplicado un test de asociación, Chi-cuadrado, entre variables categóricas (Sokal & Rohlf, 1995).

TABLA 1. Frecuencia de ocupación de especies de árboles por parte de *Dendrophylax lindenii* en Cabo San Antonio, Península de Guanahacabibes.

Especies de forofitos	No. de individuos ocupados	% en relación al total
<i>Comocladia dentata</i>	16	17,2
<i>Diospyros crassinervis</i>	12	12,9
<i>Cedrela odorata</i>	9	9,7
<i>Erythroxylum areolatum</i>	8	8,6
<i>Sideroxylon foetidissimum</i>	8	8,6
<i>Tabebuia angustata</i>	8	8,6
<i>Ficus laenigata</i>	5	5,4
<i>Plumeria tuberculata</i>	4	4,3
<i>Schaefferia frutescens</i>	4	4,3
<i>Atheramnus lucidus</i>	3	3,2
<i>Citharexylum fruticosum</i>	3	3,2
Árboles derribados no identificados	3	3,2
<i>Chascoteca neopeltandra</i>	2	2,2
<i>Stigmatophyllum sagraeanum</i>	2	2,2
Árboles secos no identificados	2	2,2
<i>Picrodendron macrocarpum</i>	1	1,1
<i>Adelia ricinella</i>	1	1,1
<i>Celtis trinervia</i>	1	1,1
<i>Drypetes alba</i>	1	1,1
Número de total individuos ocupados	93	

RESULTADOS

Selección de sustrato que manifiesta *Dendrophylax lindenii*. En los dos transectos a lo largo del bosque semidecídulo de Cabo San Antonio se contabilizaron un total de 93 individuos pertenecientes a 19 especies de forofitos ocupados por D.I. Entre los forofitos se encuentra la categoría de árbol seco (Tabla 1). Las especies con mayor grado de ocupación resultaron ser: *Comocladia dentata* con 16 individuos, *Diospyros crassinervis* con 12, *Cedrela odorata* con nueve y *Erythroxylum areolatum*, *Sideroxylon foetidissimum* y *Tabebuia angustata* con ocho. En estas seis especies se concentra el 65,6% del total de individuos ocupados, el resto muestra bajos niveles de ocupación aún cuando son localmente abundantes.

Los mayores porcentajes de ocupación los presentan *Comocladia dentata* con el 17,2% del total de ocupados y *Diospyros crassinervis* con el 12,9% del total de individuos. Este resultado pudiera estar apuntando a una relación más estrecha con estas dos primeras especies en relación al resto.

Un total de 344 individuos de D.I. fueron localizados.

Las especies de forofitos con mayor número de individuos de esta orquídea epífita se encontraron en *Comocladia dentata* con 24,4% de D.I. y una ocupación media de 5,3 individuos por forofito, *Sideroxylon foetidissimum* con el 10,8% y 4,6, *Diospyros crassinervis* con el 9,9% y 2,8, y *Tabebuia angustata* con 9,3% y 4 respectivamente. En estas cuatro especies en su conjunto se concentra el 54,4% de todos los individuos de esta especie de orquídea. Esto las convierte en las especies claves para el mantenimiento y conservación de D.I. (Tabla 2).

Las especies de forofitos con los valores de ocupación media más altos de D.I. fueron *Picrodendron macrocarpum* con diez y *Chascoteca neopeltandra* con siete, concentrándose en uno y dos individuos ocupados respectivamente. Este fenómeno indica que especies de forofitos con bajo número de individuos ocupados pueden tener un alto número de individuos de una especie epífita.

Otro aspecto interesante era conocer cómo se comporta la distribución de los individuos de D.I. sobre los individuos de cada especie de forofito con más del 5% (Migenis & Ackerman, 1993) de sus individuos

TABLA 2. Comparación del número de individuos de *Dendrophylax lindenii* en cada especie de forofito y su densidad media en Cabo San Antonio, Península de Guanahacabibes.

Especies de forofitos	No. de individuos de <i>D. lindenii</i>	% del total de individuos	Ocupación media + s.d.
<i>Comocladia dentata</i>	84	24,4	5,3 + 5,9
<i>Sideroxylon foetidissimum</i>	37	10,8	4,6 + 5,8
<i>Diospyros crassinervis</i>	34	9,9	2,8 + 8,5
<i>Tabebuia angustata</i>	32	9,3	4 + 7,3
<i>Cedrela odorata</i>	23	6,7	2,6 + 10
<i>Plumeria tuberculata</i>	20	5,8	6,7 + 3,5
<i>Schaefferia frutescens</i>	19	5,5	4,8 + 7,2
<i>Chascoteca neopeltandra</i>	14	4,1	7 + 13
<i>Ficus laenigata</i>	13	3,8	2,6 + 4,7
<i>Erythroxylum areolatum</i>	12	3,5	1,5 + 0,7
<i>Picrodendron macrocarpum</i>	10	2,9	10*
<i>Citharexylum fruticosum</i>	10	2,9	3,3 + 3,9
Árboles derribados	9	2,6	3 + 15
<i>Atheramnus lucidus</i>	8	2,3	2,7 + 2,4
<i>Stigmatophyllum sagraeanum</i>	7	2,1	3,5 + 1,5
Árbol seco	6	1,74	3 + 6,1
<i>Adelia ricinella</i>	2	0,6	2*
<i>Drypetes alba</i>	2	0,6	2*
<i>Celtis trinervis</i>	2	0,6	2*
Total	344		

ocupados. Al analizar la ocupación interna, se observa un alto grado de asimetría en la distribución de los individuos de D.I. sobre estos forofitos. Esta asimetría está asociada a una alta variabilidad en el grado de ocupación entre los individuos de una misma especie de forofito, lo cual provoca que sólo se encontrara diferencias significativas en la ocupación media de D.I. entre *Erythroxylum areolatum* y *Comocladia dentata* (Chi-sq 13.13, $p < 0.041$) (Fig. 1).

Altura y DBH de los forofitos. Existe una variabilidad interna entre los individuos de las especies con mayor grado de ocupación de D.I. tanto en relación a su altura como al DBH.

El individuo de menor altura ocupado resultó ser un juvenil de *Atheramnus lucidus* de solo de 2 m, mientras el más alto lo fue un individuo de 17 m de *Sideroxylon foetidissimum*. Es precisamente esta última especie la que presenta los valores medios de altura más altos.

La Figura 2 muestra la distribución de la altura media de los individuos de las distintas especies de forofitos con más de un 5% de ocupación por parte

de D.I. En este caso el patrón es complejo mostrando globalmente diferencias de inserción altamente significativas (Chi-sq. 22.54, $p < 0.001$). Para cuatro de las especies de forofitos (*Cedrela odorata*, *Diospyros crassinervis*, *Tabebuia angustata* y *Ficus laenigata*) no hubo diferencias en la altura media. Sin embargo, en *Erythroxylum areolatum* esta es significativamente menor que en *Sideroxylon foetidissimum* y de igual forma *Comocladia dentata* presenta una altura media menor que *Ficus laenigata* y *Sideroxylon foetidissimum*.

La variabilidad de inserción de D.I. en relación al tamaño (DBH) de los forofitos es altamente significativa (Chi-sq 31.59, $p < 0.0001$) (Fig. 3). Es *Ficus laenigata* quien se diferencia significativamente de todas las demás, pues mientras que su DBH es cercano a una media de 70 cm, en el resto de las especies está entre 20 y 30 cm mayormente. Los rangos extremos de los individuos ocupados fueron de 4 cm en individuos de *Diospyros crassinervis* y la máxima, 110 cm, corresponde a individuos de *Ficus laenigata*.

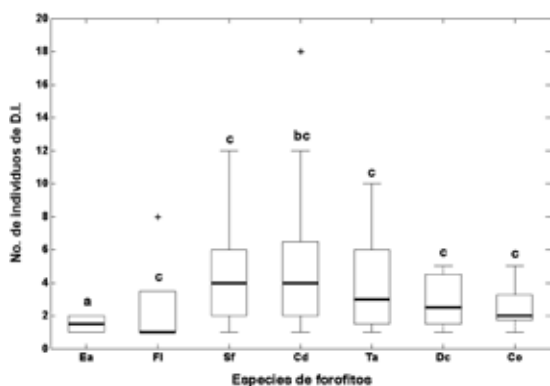


FIGURA 1. Distribución de *Dendrophyllax lindenii* en los forofitos con más de 5% de ocupación. (Ea= *Erythroxyllum areolatum*; Fl= *Ficus laenigata*; Sf= *Sideroxyllon foetidissimum*; Cd= *Comocladia dentata*; Ta= *Tabebuia angustata*; Dc= *Diospyros crassinervis*; Co= *Cedrela odorata*).

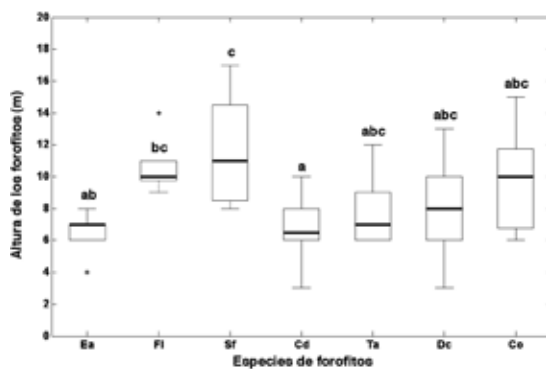


FIGURA 2. Distribución de las alturas de los forofitos de las especies con más de 5% de ocupación donde se inserta *Dendrophyllax lindenii*. (Ea= *Erythroxyllum areolatum*; Fl= *Ficus laenigata*; Sf= *Sideroxyllon foetidissimum*; Cd= *Comocladia dentata*; Ta= *Tabebuia angustata*; Dc= *Diospyros crassinervis*; Co= *Cedrela odorata*).

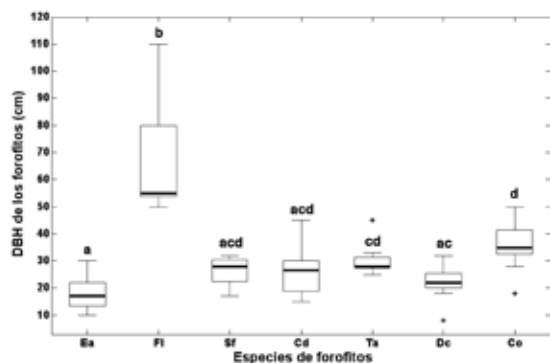


FIGURA 3. Distribución del DBH de los forofitos de las especies con más de 5% de ocupación donde se inserta *Dendrophyllax lindenii*. (Ea= *Erythroxyllum areolatum*; Fl= *Ficus laenigata*; Sf= *Sideroxyllon foetidissimum*; Cd= *Comocladia dentata*; Ta= *Tabebuia angustata*; Dc= *Diospyros crassinervis*; Co= *Cedrela odorata*).

DISCUSIÓN

Los estudios sobre la especificidad de la relación de las epífitas con sus forofitos son pocos, y no concluyentes siendo aun un tema abierto (Trapnell & Hamrick, 2006). Algunos estudios encuentran una baja especificidad entre las epífitas y los forofitos donde habitan (Johansson, 1974; Stanford, 1974; Todzia, 1986; Ackerman *et al.*, 1989; Zimmerman & Olmsted, 1992; Ackerman *et al.*, 1996), mientras otros muestran una fuerte asociación (Went, 1940;

Frei, 1973; ter Steege & Cornelissen, 1989; Merwin *et al.*, 2003). La fuerte asociación que muestran las especies de orquídeas con determinadas especies de forofitos pudiera indicar una especificidad orquídea-forofito. Trapnell & Hamrick (2006) en sus estudios en Costa Rica con *Laelia rubescens* encontraron una asociación entre esta especie y *Samanea saman*. Sin embargo, mientras unos hospederos presentaban altos índices de colonización por esta orquídea, otros cercanos, de igual porte y supuestamente igual edad, se encontraban totalmente vacíos.

En este estudio hemos encontrado que la especie de orquídea epífita, *Dendrophyllax lindenii*, muestra una estrategia generalista en la selección del sustrato (tipo de forofito) pues se ha encontrado en 19 especies de forofitos diferentes. Sin embargo, dentro de esta estrategia generalista, muestra una clara tendencia por determinados forofitos como: *Comocladia dentata*, *Diospyros crassinervis* y *Cedrela odorata*. Esta misma estrategia generalista la encontramos también en cuanto a la altura y DBH de los forofitos que ocupa donde observamos una alta variabilidad tanto dentro de cada forofito determinado como entre todos ellos.

En nuestro estudio hemos encontrado un área basal mínima (aproximadamente < 15-20 cm) por debajo de la cual es altamente improbable la

colonización de los forofitos. Una de las razones de esta estrategia generalista de *Dendrophylax lindenii* pudiera ser la casi total ausencia de otras especies de orquídeas epífitas sobre estas especies de forofitos, lo cual podría indicar ausencia y/o poca importancia de efectos denso-dependientes en la selección de hábitat por parte de esta orquídea epífita. En general, se ha apuntado que las epífitas vasculares presentan bajos niveles de competencia intra e interespecifica (Zotz & Hietz, 2001). *Comocladia dentata* presenta el mayor porcentaje de ocupación de las seis especies más abundantes y el mayor número de árboles ocupados (16 árboles ocupados de los 32 censados) lo cual pudiera estar indicando una preferencia marcada de *Dendrophylax lindenii* por esta especie. En el resto de las especies de forofitos se ha encontrado un gran número de ellos de igual porte y supuestamente igual edad totalmente vacíos, lo cual indica en estos casos que no existe una especiación por parte de esta especie de orquídea.

El establecimiento de las semillas de las orquídeas en el sustrato depende de muchos factores bióticos y abióticos. El factor biótico más crítico es la presencia de las micorrizas en el sustrato al cual llegan (Trapnell & Hamrick, 2006). La dependencia de hongos micorrícicos para la germinación es un importante componente de la biología de las orquídeas (Arditti, 1992) y pueden limitar la distribución de muchas especies (Clements, 1987), así como el reclutamiento de nuevos individuos en las poblaciones. En la Península de Guanahacabibes el establecimiento de las semillas pudiera verse limitado por la presencia de líquenes y especies de Tillandsias muy comunes sobre determinadas especies arbóreas. Migenis & Ackerman (1993) en sus estudios con las orquídeas epífitas de Bisley Watersheds, Puerto Rico, no encontraron una especificidad entre las especies de orquídeas presentes en esa área y las especies de forofitos. Apuntan además, que sus datos sugieren una preferencia, como en nuestro caso, por determinadas especies de forofitos pero no una relación especie de orquídea-especie de forofito. Tremblay *et al.* (1998) encontraron que *Lepanthes caritensis* en Puerto Rico solamente coloniza forofitos de la especie *Micropholis guyanensis* reconociendo que es un fenómeno raro en orquídeas epífitas, apuntando

además que solo el 7% de los forofitos de esta especie resultan colonizados, siendo esta la especie de forofito más abundante en el área de estudio. Coincidimos con estos autores, en que pueden ser varias las razones para que se produzca este fenómeno. Pudiera ser que las semillas no hayan llegado a colonizar estos potenciales forofitos, lo cual a juzgar por la distribución en las áreas estudiadas, parece improbable, pues sería casi imposible que las semillas colonicen a forofitos de igual especie y tamaño de forma intermitente, dejando otros de por medio totalmente vacíos. Ya desde principios del siglo pasado se conoce que las semillas de las orquídeas dependen de determinados hongos para su germinación (Bernard, 1909). Incluso, se apunta, que el desarrollo de la interacción con las micorrizas ha sido y es un evento crucial en la evolución de la familia Orchidaceae.

Bayman *et al.* (2002) apuntan que pocos estudios se han desarrollado en este aspecto en orquídeas epífitas, ya que el diminuto tamaño de las semillas dificulta los experimentos. Estos autores en sus estudios con la especie epífita *Lepanthes rupestris* en Puerto Rico encontraron que en la misma los hongos ejercen tanto efectos positivos, como negativos, en el crecimiento y supervivencia de las plantas de esta especie. Tremblay *et al.* (1998) opinan que la asociación encontrada entre orquídeas y algunas especies de musgos sugiere que la especificidad de las orquídeas por determinadas especies y tamaños de forofitos pudiera estar dada por la acumulación de esos musgos en esas especies con lo cual se concuerda plenamente. En nuestro caso parece ocurrir igual fenómeno. Todo parece indicar, que *Dendrophylax lindenii* no elige los forofitos donde se asentará, sino, que depende de la presencia de las micorrizas para su establecimiento, razón, que parece ser la más acertada. Dada la diversidad de especies de forofitos que ocupa y la variabilidad, tanto en altura como en el DBH de las mismas, se demuestra que *Dendrophylax lindenii* no muestra predilección por forofitos de determinada especie. En otras palabras, coloniza aquellos forofitos, sin distinción de especie, altura o DBH, sobre los cuales se encuentran las micorrizas. La razón de que determinadas especies sean las más frecuentes en esta relación pudiera ser una mayor asociación

de las micorrizas con las mismas, lo que provoca una mayor presencia de individuos de *Dendrophylax lindenii* sobre ellas.

La alta incidencia de *Dendrophylax lindenii* sobre determinadas especies de forofitos sugiere que un manejo cuidadoso de las mismas es fundamental para el establecimiento y permanencia de esta especie en la Península de Guanahacabibes. Tanto *Diospyros crassinervis* como *Cedrela odorata* son altamente cotizadas como maderas preciosas y un manejo cuidadoso de sus poblaciones se hace esencial para la conservación de *Dendrophylax lindenii*.

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ORQUIDEOFLÓRULA DE UN SECTOR DE SERRANÍA DE LA CUCHILLA, MUNICIPIO CARIPE, ESTADO MONAGAS, VENEZUELA

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RESUMEN. A fin de contribuir con el conocimiento de la familia Orchidaceae en el Macizo del Turimiquire, se realizaron exploraciones en un sector de la Serranía de La Cuchilla, municipio Caripe, estado Monagas (10°07,00'N 63°33,45'O) entre los años 2005-2008 y durante los meses de diciembre-enero, mayo, julio-septiembre. Todos los ejemplares colectados están depositados en IRBR con duplicados en VEN. Se identificaron 47 especies en 30 géneros. Los géneros más importantes son: *Epidendrum* (8 spp.), *Pleurothallis s.l.* (3 spp.) y *Prosthechea* (3 spp.), y las especies más frecuentes fueron: *Epidendrum subpurum*, *Acianthera lanceana* y *Scaphyglottis fusiformis*. Así mismo, se señalan un nuevo reporte para la porción oriental de la Cordillera de la Costa: *Acianthera miqueliana*. Finalmente, el 20% de las especies mencionadas está señalado en el Libro Rojo de la Flora Venezolana: una en peligro crítico (*Cattleya gaskelliana*), tres especies vulnerables, una en peligro tres en menor riesgo/casi amenazadas y una (*Prosthechea venezuelana*) como insuficientemente conocida. Se presentan fotografías de algunas de las especies encontradas y una clave para su identificación.

ABSTRACT. To contribute with the study of the Orchidaceae on El Macizo Montañoso del Turimiquire, field exploration was done in a sector of the Serranía de La Cuchilla, Caripe municipality, Monagas state (10°07,00'N 63°33,45'O), during the years 2005-2008, in the months of December-January, May and July-September. Collected specimens were housed in the Herbarium IRBR with duplicates at VEN. As result, 47 species in 30 genera were identified. The most important genera are *Epidendrum* (8 spp.), *Pleurothallis s.l.* (3 spp.) and *Prosthechea* (3 spp.); the most frequent species are: *Epidendrum subpurum*, *Acianthera lanceana* y *Scaphyglottis fusiformis*. Additionally, a new record to the east portion of Cordillera de la Costa is reported: *Acianthera miqueliana*. Finally, 20% of species are mentioned in the Red Book of Venezuelan Flora: one in critic danger (*Cattleya gaskelliana*), three as vulnerable, one in danger, three as minor risk, and one (*Prosthechea venezuelana*) as insufficiently known. An identification key to the species and pictures of some of the taxa are presented.

PALABRAS CLAVES / KEY WORDS: Orchidaceae, Florística, Floristic, Macizo del Turimiquire, Monagas, Venezuela

La familia Orchidaceae es uno de los grupos de Magnoliophyta más ampliamente distribuido a nivel mundial (Dressler 1981); así, como uno de los más diversos, con más de 24 000 especies (Chase *et al.* 2003), la mayoría de éstas en el continente americano, especialmente en la cordillera andina (Dressler, 1981; Carnevali *et al.* 2007). En Venezuela, esta familia alcanza aproximadamente 1612 especies en 222 géneros (Carnevali *et al.*, 2007), siendo las áreas con el mayor número de especies la Cordillera de Mérida y la Sierra de Perijá, que en conjunto poseen una orquideoflora compuesta por más de 818 especies, seguidas de la Guayana venezolana con más de 700 especies (Carnevali *et al.* 2003, 2007).

En el nororiente de Venezuela se han realizado algunos trabajos donde se han producido listas de especies. Entre ellos destacan las exploraciones de Steyermark al cerro Turimiquire y la región oriental adyacente (Schweinfurt 1957; Steyermark 1966), las referencias presentadas por Dunsterville y Garay (1959, 1961, 1965, 1966, 1972, 1976) a lo largo de su obra a colecciones realizadas en Caripe y áreas adyacentes, los reportes de Foldats (1969, 1970a, 1970b, 1970c, 1970d) de las colecciones realizadas por varios exploradores en el Macizo del Turimiquire, el listado de especies para el Parque Nacional El Guácharo presentado por Lárez (2003), entre otros. Sin embargo, estas exploraciones usualmente involucran todos los componentes de la

flora, por lo que hasta ahora, en el nororiente y muy especialmente en el Macizo del Turimiquire no es posible establecer cuál es el nivel real de conocimiento de la familia Orchidaceae. En este sentido, se presenta un listado, tentativo, de las especies de orquídeas presentes en un sector de la Serranía de la Cuchilla, sur del Macizo Montañoso del Turimiquire, en un área cercana al Parque Nacional El Guácharo.

Materiales y métodos

Área de estudio

Las muestras se colectaron en La Hacienda La Cuchilla (Fig. 1A), que se encuentra en la Serranía de la Cuchilla (sur del Macizo del Turimiquire), al sur del municipio Caripe, en los límites con el municipio Piar (10°07'00"N 63°33'45"O), estado Monagas, Venezuela. Altitudinalmente, se ubica entre los 900-1200 m snm. Desde el punto de vista climático, tiene temperaturas que oscilan entre los 12 y los 24 °C. Las precipitaciones alcanzan 1124 mm anuales, presentando un claro patrón de biestacional, con un período de sequía que va desde enero hasta mayo y uno lluvioso que va desde junio hasta diciembre [datos climáticos desde [http://venciclopedia.com/index.php?title=Municipio_Caripe_\(Monagas\)](http://venciclopedia.com/index.php?title=Municipio_Caripe_(Monagas))].

Métodos

Entre los años 2005-2008, durante los meses de diciembre-enero, mayo, julio-septiembre, se realizaron exploraciones dentro de los límites de los cafetales, considerándose especies terrestres, epífitas o litófitas. Las epífitas, generalmente, se colectaron de las ramas de árboles caídos. Todas las especies colectadas fueron mantenidas en cultivo, teniendo especial cuidado con aquellas que al momento de colección no se encontraban en fenofase reproductiva. Las muestras para herbario se tomaron generalmente en dos partes, una para la *exsiccata*, que se procesó según las técnicas tradicionales para la preparación de muestras de herbario (Lindorf *et al.*, 1999) y otra constituida sólo de flores, que fueron fijadas en FAA, de las que se utilizó parte durante la identificación. El material fue identificado con la ayuda de las obras de Foldats (1969, 1970a, 1970b, 1970c, 1970d), Steyermark y Huber (1978), Luer (1986a, 1986b), Romero y Carnevali (2000) y Carnevali *et al.* (2003). De forma general se sigue el sistema propuesto por Pridgeon *et al.* (2003, 2005, 2009). Las fotografías

fueron tomadas por el autor en condiciones de campo o cultivo. Las muestras colectadas fueron depositadas en el IRBR con duplicados en VEN [testigos de herbario: *Leopardi s.n* (todas las muestras en líquido año 2005-2006 y parte de las de 2007-2008), *Leopardi et al.* 150-207, 300-313].

Resultados y discusión

Se identificaron 47 especies de Orchidaceae en 30 géneros; siendo los mejor representados *Epidendrum* L. (8 spp.), *Pleurothallis* R. Br. *s.l.* (3 spp.) y *Prosthechea* Knowles & Westc. (3 spp.) (Tabla 1). La mayor parte de las especies reportadas son epífitas. El forofito (hospedero) más frecuente son los Guamos (*Inga* spp.); sin embargo, los forofitos con mayor diversidad usualmente son los árboles de gran tamaño, como el Bucare (*Erythrina* sp.), Angelino (*Homalium* sp.), entre otros.

Las especies más frecuentes son *Epidendrum subpurum* Rchb. f., *Acianthera lanceana* (Lodd.) Pridgeon & M.W. Chase y *Scaphyglottis fusiformis* (Griseb.) Schult. Otras como *Epidendrum secundum* Jacq. o *Cyrtopodium* aff. *willmorei* Knowles & Westc., se encuentran sólo en las porciones sabanizadas de la serranía y algunas especies como *Govenia utriculata* (Sw.) Lindl. prefieren lugares sombreados con alta cantidad de materia orgánica.

La alta proporción de especies epífitas con respecto a las terrestres/litófitas ya ha sido señalada por Gentry y Dodson (1987) al indicar que más del 70% de las especies conocidas de orquídeas prefieren esa forma de vida; aunado a esto, las prácticas culturales para la manutención de los cafetales tienden a eliminar las plantas que crecen en el suelo, encontrándose éstas sólo en lugares protegidos, entre raíces tabulares de algunos árboles, muy cerca de troncos de árboles en descomposición (usualmente sobre o tendiendo a estar debajo de ellos) o en lugares no cultivados, a veces cerca de los caminos, como es el caso de *Epidendrum secundum*.

Por otro lado, la alta frecuencia de algunas plantas como *Epidendrum subpurum* o *Acianthera lanceana* podría asociarse al carácter secundario de la vegetación y a las características microclimáticas asociadas a los distintos hábitats, ya que géneros como *Dichaea* Lindl. tienen tendencia a crecer en lugares sombríos y húmedos, que no siempre están garantizados en los cafetales, por lo que usualmente se les puede encontrar en la zona límite

Tabla 1. Orchidaceae en la Hacienda La Cuchilla, municipio Caripe, estado Monagas, Venezuela.

Nombre Científico	S	EC
<i>Acianthera lanceana</i> (Lodd. ex Lindl.) Pridgeon & M.W.Chase	E	MR/ca
<i>A. miqueliana</i> * (Lodd. ex Lindl.) Pridgeon & M.W.Chase	E	-
<i>A. rubroviridis</i> (Carnevali & G.A. Romero) Carnevali & G.A. Romero	E	-
<i>Anathallis sclerophylla</i> (Lindl.) Pridgeon & M.W. Chase	E	-
<i>Brassia wagneri</i> Rchb.f.	E	-
<i>Camaridium micranthum</i> M. A. Blanco.	E	-
<i>Camaridium ochroleucum</i> Lindl.	E	-
<i>Campylocentrum micranthum</i> (Lindl.) Rolfe	E	-
<i>Cattleya gaskelliana</i> Rchb.f.	E	CR
<i>Cyrtopodium</i> aff. <i>willmorei</i> Knowles & Westc.	T	-
<i>Dimerandra emarginata</i> (G.Mey.) Hoehne	E	-
<i>Elleanthus graminifolius</i> (Barb.Rodr.) Løjtnant	E	-
<i>Encyclia cordigera</i> (Kunth) Dressler	E	VU
<i>Epidendrum anceps</i> Jacq.	E	-
<i>E. ciliare</i> L.	E	-
<i>E. ferrugineum</i> Ruiz & Pav.	E	-
<i>E. ramosum</i> Jacq.	E	-
<i>E. rigidum</i> Jacq.	E/L	-
<i>E. secundum</i> vel sp. aff. Jacq.	E/T	-
<i>Epidendrum</i> aff. <i>siphonosepalum</i> Garay & Dunst.	E	-
<i>E. subpurum</i> Rchb.f.	E	-
<i>Gomesa bicolor</i> (Lindl.) M.W.Chase & N.H.Williams	E	VU
<i>Gongora maculata</i> Lindl.	E	-
<i>Govenia utriculata</i> vel sp. aff. (Sw.) Lindl.	T	-
<i>Isochilus linearis</i> (Jacq.) R.Br.	E	-
<i>Jacquinella globosa</i> (Jacq.) Schltr.	E	-
<i>J. teretifolia</i> (Sw.) Britton & P. Wilson	E	-
<i>Leochilus labiatus</i> (Sw.) Kuntze	E	-
<i>Lockhartia</i> sp.	E	-
<i>Maxillaria porrecta</i> Lindl.	E	-
<i>Maxillariella caespitifica</i> (Rchb.f.) M. A. Blanco & Carnevali	E	-
<i>Mormodes atropurpurea</i> Lindl.	ED	EP
<i>Mormodes</i> sp.	ED	-
<i>Oeceoclades maculata</i> (Lindl.) Lindl.	T	-
<i>O. obryzatum</i> Rchb.f. & Warsz.	E	-
<i>Pleurothallis discoidea</i> Lindl.	E	-
<i>P. pruinosa</i> Lindl.	E	-
<i>P. revoluta</i> (Ruiz & Pav.) Garay	E	-
<i>Polystachya foliosa</i> (Hook.) Rchb.f.	E	-
<i>Prosthechea chacaoensis</i> (Rchb.f.) W.E.Higgins	E	MR/ca
<i>P. livida</i> (Lindl.) W.E.Higgins	E	-
<i>P. venezuelana</i> (Schltr.) W.E.Higgins	E	IC
<i>Rodriguezia lanceolata</i> Ruiz & Pav.	E	MR/ca
<i>Scaphyglottis fusiformis</i> (Griseb.) R.E.Schult.	E	-
<i>Stanhopea wardii</i> Lodd. ex Lindl.	E	VU
<i>Stelis cucullata</i> Ames	E	-
<i>S. pygmaea</i> Cogn.	E	-

+ = nuevo registro para el Macizo del Turimiquire

S = sustrato; E = epífita; T = terrestre; L = litófito; ED = epífita en troncos en descomposición.

EC = Sistema de categorías de la Lista Roja, según Llamozas *et al.* (2003); MR/ca = menor riesgo/casi amenazada; CR = peligro crítico; EP = En Peligro; VU = vulnerable; IC = insuficientemente conocida; - = no hay datos disponibles.

entre el cafetal y el área boscosa no cultivada.

Es notable que, a pesar de que el área estudiada involucra menos de 100 ha, cuando se compara con otros trabajos realizados en el municipio Caripe o áreas cercanas, la diferencia en el número de especies reportadas es considerable; así, Steyermark en su exploración al cerro Turimiquire y región oriental adyacente reporta 61 especies repartidas entre los estados Anzoátegui (34 spp.), Monagas (24 spp.) y Sucre (11 spp.), siendo las de Sucre colectadas casi todas (10 spp.) en el Cerro Turimiquire y las de Monagas en su mayoría (21 spp.) en el municipio Caripe y una de ellas, *Sacoila lanceolata* (Aubl.) Garay [como *Spiranthes orchioides* (Sw.) A. Rich. en Schweinfurth, Fieldiana, Bot. 28 (3-4): 862. 1957], en las sabanas de la Serranía de La Cuchilla (Schweinfurth 1957).

En exploraciones posteriores al Cerro Turimiquire, Steyermark refiere una lista de 17 especies (Steyermark 1966), mientras que Figueroa (1992) menciona 8 especies para la flórula del Cerro de la Cueva del Guácharo (Parque Nacional El Guácharo); posteriormente, Lárez (2003) señala 11 spp. para el Parque Nacional el Guácharo; en general, las especies mencionadas por Lárez (2003) y Figueroa (1992) coinciden con las reportadas por Steyermark (1966). De los trabajos publicados, el que tiene el número más cercano a lo reportado en este trabajo es el Foldats (1969, 1970a, 1970b, 1970c, 1970d) que recopilando todas las colecciones realizadas hasta los años 60 menciona ca. 37 especies para el municipio Caripe. Lo antes señalado podría atribuirse al esfuerzo de colección de los distintos autores; al respecto, Carnevali *et al.* (2007) comentan que independientemente de lo bien que haya sido trabajada un área por botánicos convencionales, dado lo críptico de la mayoría de las especies de orquídeas, cuando un botánico especializado en Orchidaceae

explora sistemáticamente esa misma área, usualmente aparecen nuevos registros para la flora local, esto está en concordancia con Lárez (2005), que señala que el hábito epífito de estas plantas dificulta su colección.

Al revisar la distribución de las plantas, una resultó nueva para la región nororiental del país: *Acianthera miqueliana* (H. Focke) Pridgeon & M.W.Chase que según Carnevali *et al.* (2003) ha sido colectada fuera de la Guayana venezolana en la porción central y occidental de la Cordillera de la Costa; sin embargo, existe la posibilidad de que esta entidad pueda ser una especie muy afín, *Acianthera angustifolia* (Lindl.) Luer, que también ha sido colectada en la porción central de la cordillera de la costa (G. Carnevali, com. pers. 2009).

Cuando se revisa la lista de familias con el mayor número de especies para el estado Monagas, publicada por Lárez (2005), se aprecia la ausencia de la familia Orchidaceae, que considerando sólo las especies señaladas en este trabajo, pasaría a estar en el noveno lugar de importancia para el estado y al menos, en el tercer lugar de importancia para la Cordillera de la Costa, esto considerando la información proporcionada por Lárez (2005) sobre los principales ecosistemas del estado Monagas (Llanos, Piedemonte y Cordillera de la Costa).

Finalmente, al revisar el estado de conservación de las especies señaladas en el Libro Rojo de la Flora Venezolana (Llamozas *et al.* 2003), se encuentra que el 20% está bajo alguna categoría (Tabla 1). Resulta inquietante que una está en peligro crítico: *Cattleya gaskelliana* Rehb. f., endémica del Macizo del Turimiquire; aparte, 3 están catalogadas como vulnerables, 1 está catalogada En Peligro (*Mormodes atropurpurea* Lindl.), 3 como menor riesgo/casi amenazadas y una [*Prosthechea venezuelana* (Schltr.) W.E. Higgins] como insuficientemente conocida.

CLAVE PARA LA IDENTIFICACIÓN DE LAS ESPECIES

- 1a. Hojas teretes, triquetras (de contorno circular o triangular) o lateralmente aplanadas 2
- 1b. Hojas dorsiventralmente aplanadas 4
- 2a. Hojas lateralmente aplanadas, imbricadas *Lockhartia* sp.
- 2b. Hojas teretes o algo triquetras, no imbricadas 3
- 3a. Plantas de menos de 7 cm de alto. Inflorescencia sin brácteas foliáceas en su ápice *Jacquiiniella globosa*
- 3b. Plantas de más 10 cm de alto. Inflorescencia con 1--2 brácteas foliáceas en su ápice *Jacquiiniella teretifolia*

4a.	Pseudobulbos ausentes	5
4b.	Pseudobulbos presentes.....	24
5a.	Crecimiento monopodial	6
5b.	Crecimiento simpodial	7
6a.	Flores generalmente solitarias; labelo sin espolón	<i>Epidendrum</i> aff. <i>siphonosepalum</i>
6b.	Flores en racimos; labelo espolonado	<i>Campylocentrum micranthum</i>
7a.	Ovario no articulado con el pedicelo	8
7b.	Ovario articulado con el pedicelo	16
8a.	Labelo libre de la columna	9
8b.	Labelo unido a la columna	11
9a.	Flores agrupadas en inflorescencia espiciforme. Brácteas conspicuas, cubriendo a las flores. Flores blancas	<i>Elleanthus graminifolius</i>
9b.	Flores solitarias, sucesivas, raramente 2. Brácteas inconspicuas. Flores rosadas	10
10a.	Tallos secundarios ligeramente engrosados. Hojas de más de 0.5 cm de ancho. Flor de más de 1 cm de diámetro; labelo basalmente con un callo compuesto por una serie de lamelas transversales	<i>Dimerandra emarginata</i>
10b.	Tallos secundarios no engrosados. Hojas de hasta 0.3 cm de ancho. Flor de menos de 0.6 cm de diámetro; labelo ecaloso	<i>Isochilus linearis</i>
11a.	Labelo simple	12
11b.	Labelo 3-lobulado	13
12a.	Ovario con una vesícula alargada en su ápice	<i>Epidendrum ramosum</i>
12b.	Ovario sin una vesícula alargada en su ápice	<i>Epidendrum rigidum</i>
13a.	Inflorescencia péndula. Lóbulo medio del labelo agudo	<i>Epidendrum ferrugineum</i>
13b.	Inflorescencia erecta. Lóbulo medio del labelo truncado-retuso hasta emarginado	14
14a.	Inflorescencia racemosa. Labelo con márgenes irregularmente dentado-laciniados	<i>Epidendrum secundum</i> vel aff.
14b.	Inflorescencia racemosa o paniculada. Labelo con márgenes enteros	15
15a.	Hojas oblongas. Inflorescencia subcapitada	<i>Epidendrum anceps</i>
15b.	Hojas lineares. Inflorescencia no subcapitada	<i>Epidendrum subpurum</i>
16a.	Sépalos unidos entre sí, flores de contorno triangular	17
16b.	Sépalos libres o unidos, flores nunca de contorno triangular	18
17a.	Inflorescencia con menos de 4 flores, laxas. Labelo apiculado	<i>Stelis pygmaea</i>
17b.	Inflorescencia con más de 6 flores. Labelo obtuso	<i>Stelis cucullata</i>
18a.	Cara externa de los sépalos hirsuta o tuberculada	19
18b.	Cara externa de los sépalos glabra	20
19a.	Inflorescencia racemosa con más de 4 flores. Pétalos lanceolados con los márgenes fimbriados. Ovario glabro	<i>Acianthera lanceana</i>
19b.	Inflorescencia fasciculada, con 1--3 flores. Pétalos flabelados de márgenes enteros. Ovario pubescente	<i>Acianthera rubroviridis</i>
20a.	Rizoma alargado, ramicales visiblemente separados entre sí. Hojas moradas	<i>Acianthera miqueliana</i>
20b.	Rizoma abreviado, ramicales muy juntos. Hojas generalmente verdes	21
21a.	Flores amarillas, sucesivas o raro 2	<i>Pleurothallis discoidea</i>
21b.	Flores blanquecinas y con antesis simultánea	22
22a.	Plantas con menos de 6 cm de alto. Inflorescencia de 2--4 flores	<i>Pleurothallis pruinosa</i>
22b.	Plantas con más de 7 cm de alto. Inflorescencia con más de 6 flores	23
23a.	Sépalos glabros en su cara interna; pétalos linear-filiformes, de longitud similar a la de los sépalos; labelo geniculado	<i>Pleurothallis revoluta</i>

23b.	Sépalos pubescentes en su cara interna; pétalos elípticos, más pequeños que los sépalos; labelo no geniculado	<i>Anathallis sclerophylla</i>
24a.	Labelo unido a la columna, profundamente 3-lobulado; lóbulo medio acicular, lóbulos laterales con el margen externo irregularmente laciniado	<i>Epidendrum ciliare</i>
24b.	Labelo sin la combinación anterior de caracteres	25
25a.	Plantas terrestres	26
25b.	Plantas epífitas	30
26a.	Pseudobulbos con uno de los entrenudos más grande que los demás. Hojas maculadas	<i>Oeceoclades maculata</i>
26b.	Pseudobulbos o cormos con los entrenudos de tamaño similar. Hojas no maculadas	27
27a.	Cormos hipógeos. Pseudobulbos ausentes. Hojas 2	<i>Govenia utriculata</i> vel aff.
27b.	Cormos hipógeos ausentes. Pseudobulbos presentes. Hojas 3 ó más	28
28a.	Pseudobulbos de más de 15 cm de largo. Labelo verrugoso	<i>Cyrtopodium</i> aff. <i>willmorei</i>
28b.	Pseudobulbos de menos de 12 cm de largo. Labelo no verrugoso	29
29a.	Inflorescencias multifloras, más largas que el pseudobulbo. Flores de color púrpura intenso. Labelo cuando aplanado conspicuamente 3-lobulado	<i>Mormodes atropurpurea</i>
29b.	Inflorescencias multifloras, más cortas que el pseudobulbo. Flores amarillas. Labelo cuando aplanado, ligeramente 3-lobulado	<i>Mormodes</i> sp.
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31a.	Flores amarillas-marrones, con manchas pardo-rojizas; pétalos linear-lanceolados, de márgenes enteros, basalmente fusionados con la columna; labelo sin una mancha parecida a un ojo a cada lado de su porción basal, mesoquilo no desarrollado	<i>Gongora maculata</i>
31b.	Flores amarillas; pétalos aovado-elípticos, márgenes ondeado-rizados, no fusionados con la columna; labelo con una mancha parecida a un ojo a cada lado de su porción basal, mesoquilo desarrollado	<i>Stanhopea wardii</i>
32a.	Tallos secundarios sobrepuestos	<i>Scaphyglottis fusiformis</i>
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33a.	Inflorescencia terminal	34
33b.	Inflorescencia basal o en las vainas de las hojas jóvenes, pero nunca terminal	39
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35a.	Flores resupinadas, más de 1 cm de diámetro; labelo con una mancha púrpura en la base del lóbulo medio	<i>Encyclia cordigera</i>
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36a.	Flores resupinadas	37
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37a.	Flores moradas, más de 3 cm de diámetro; labelo no verrugoso	<i>Cattleya gaskelliana</i>
37b.	Flores blanco-cremoso con detalles marrones, menos de 1 cm de diámetro; labelo conspicuamente verrugoso	<i>Prosthechea livida</i>
38a.	Pseudobulbos 2-foliados. Callo pubescente en la base del labelo	<i>Prosthechea chacaoensis</i>
38b.	Pseudobulbos 1-foliados. Callo glabro en la base del labelo	<i>Prosthechea venezuelana</i>
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39b.	Rizoma abreviado (pseudobulbos juntos)	42
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- 40b. Flores solitarias o en fascículos. Sépalos laterales libres o connados en la base, nunca geniculados 41
- 41a. Flores solitarias o en grupos de 2; nacen en las vainas de las hojas jóvenes; sépalos laterales libres entre sí; labelo pubescente en su base *Camaridium ochroleucum*
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- 44a. Labelo simple 45
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- 45a. Plantas verdes, más de 10 cm de alto. Pseudobulbos bifoliados. Inflorescencia con más de 5 flores. Flores más de 2 cm de diámetro; labelo con el ápice acuminado *Brassia wagneri*
- 45b. Plantas rojizas, menos de 7 cm de alto. Pseudobulbos unifoliados. Inflorescencia con 2-4 flores. Flores menos de 1 cm de diámetro; labelo apicalmente emarginado *Leochilus labiatus*
- 46a. Sépalos connados; pétalos con márgenes ondulados *Gomesa bicolor*
- 46b. Sépalos libres; pétalos con márgenes enteros *Oncidium obryzatum*

Descripciones

Acianthera lanceana (Lodd. ex Lindl.) Pridgeon & M.W.Chase, Lindleyana 16(4): 244. 2001. Fig. 1B.

Epífita, cespitosa, menos de 12 cm de alto. Inflorescencia racemosa. Flores variando desde verdes hasta naranja, de menos de 1 cm de diámetro; sépalos externamente hirsutos o tuberculados, los laterales unidos en un sinsépalo bífido; pétalos lanceolados, con márgenes fimbriados. Ovario glabro. En la zona existe una variedad cleistógama. Florece entre octubre y marzo.

Acianthera miqueliana (H. Focke) Pridgeon & M.W.Chase, Lindleyana 16: 244. 2001.

Epífita, cespitosa, rizoma rastrero, cubierto por vainas. Ramicaules usualmente morados, menos de 10 cm de alto. Hojas usualmente de color purpúreo. Flores solitarias, sucesivas; sépalos laterales unidos en un sinsépalo; pétalos lanceolados, de menor tamaño que los sépalos. Florece entre agosto y noviembre. El material aquí referido, a esta especie, pudiese representar el concepto *Acianthera angustifolia* (Lindl.) Luer.

Acianthera rubroviridis (Lindl.) Pridgeon & M.W. Chase, Lindleyana 16(4): 246. 2001.

Epífita, más de 15 cm de alto. Rizoma abreviado. Flores fasciculadas, usualmente en número de dos, verdes hasta amarillentas, de menos de 1 cm de diámetro; sépalos externamente hirsutos, los laterales connados hasta más o menos la mitad de su longitud; pétalos flabelados, márgenes enteros. Ovario pubescente. Florece entre octubre y abril.

Anathallis sclerophylla (Lindl.) Pridgeon & M.W. Chase, Lindleyana 16(4): 250. 2001.

Epífita. Ramicaules de menos de 25 cm de alto. Inflorescencia racemosa, multiflora. Flores de menos de 2 cm de diámetro, blanquecinas, sépalos pubescentes en la cara interna, largamente acuminados, los laterales connados en la base; pétalos lanceolados, más pequeños que los sépalos. Florece entre julio y agosto.

Brassia wagneri Rchb.f., Bonplandia 2: 14. 1854.

Epífita. Pseudobulbos heteroblásticos, bifoliados, hojas coriáceas. Inflorescencia racemosa, basal al pseudobulbo. Flores de más de 3 cm de diámetro, verdi-amarillentas con manchas marrones, sépalos y pétalos linear-lanceolados; labelo simple, obovado-rómbico, acuminado. Florece entre marzo y mayo.

Camaridium micranthum M. A. Blanco, Lankesteriana 7(3): 520. 2007. Fig. 1C.

Epífita. Rizoma alargado (pseudobulbos muy separados) y conspicuamente cubierto de vainas. Pseudobulbos heteroblásticos, unifoliados. Inflorescencia densamente fasciculada en la base del pseudobulbo. Flores blancas, de menos de 0.5 cm de diámetro; sépalos aovado-lanceolados, los laterales connados en la base; pétalos aovado lanceolados; labelo glabro, 3-lobulado, lóbulo medio obtuso. Florece entre octubre y diciembre.

Camaridium ochroleucum Lindl., Bot. Reg. 10: t. 844. 1824.

Epífita. Rizoma alargado (pseudobulbos muy separados) y conspicuamente cubierto de vainas foliares. Pseudobulbos heteroblásticos, uni- o bifoliados. Flores solitarias o en grupos de 2; nacen en las vainas de hojas jóvenes, cerca del ápice del tallo. Flores de más de 1 cm de diámetro, blancas, labelo amarillo; sépalos y pétalos lanceolados, libres entre sí; labelo 3-lobulado, pubescente o papiloso en su base. Florece entre mayo y julio.

Campylocentrum micranthum (Lindl.) Rolfe, Orchid Rev. 11(128): 245. 1903.

Epífita, crecimiento monopodial. Hojas coriáceas. Inflorescencia racemosa; nacen por debajo de cada raíz. Flores de menos de 0.5 cm de diámetro, de color blanco hasta cremosas; labelo espolonado. Florece entre noviembre y marzo.

Cattleya gaskelliana Rchb.f., Gard. Chron., n.s. 19: 243. 1883. Fig. 1D--E.

Epífita. Pseudobulbos heteroblásticos, unifoliados. Inflorescencia racemosa de 2--5 flores, de más de 5 cm de diámetro, lila hasta blancas, fragantes, usualmente con una mancha morada hacia el ápice del labelo; labelo simple, subpandurado, en posición natural abrazando a la columna, margen apical rizado y ligeramente emarginado. Usualmente florece en mayo; sin embargo, es posible encontrar ejemplares en floración entre noviembre-diciembre.

Cyrtopodium aff. *willmorei* Knowles & Westc., Fl. Cab. 1: t. 4. 1837.

Terrestre. Pseudobulbos homoblásticos, de más de 20 cm de alto. Hojas plegadas. Inflorescencia

paniculada, basal. Flores anaranjado verdoso, con manchas pardas; labelo 3-lobulado, verrugoso. Florece en mayo.

Dimerandra emarginata (G.Mey.) Hoehne, Bol. Agric. (Sao Paulo) 34: 618. 1934.

Epífita. Rizoma abreviado. Tallos secundarios de menos de 50 cm de alto, ligeramente engrosados hasta formar cañas, los viejos a veces huecos. Hojas disticas, dispersas por el tallo. Flores rosadas, solitarias sucesivas, raro 2--3 en antesis simultánea; labelo con callo formado por una serie de lamelas transversales. Florece entre abril y junio.

Elleanthus graminifolius (Barb.Rodr.) Løjtnant, Bot. Not. 129(4): 447-448, 450, f. 2. 1977.

Epífita. Rizoma abreviado. Tallos secundarios de menos de 25 cm de alto. Hojas lineares, hacia la mitad superior del tallo secundario. Inflorescencia terminal, espiciforme; brácteas conspicuas, persistentes, de color marrón. Flores blancas, diminutas; labelo con el margen apical ciliado, columna pubescente. Florece entre diciembre y enero.

Encyclia cordigera (Kunth) Dressler, Taxon 13(7): 247. 1964.

Epífita. Rizoma abreviado. Pseudobulbos heteroblásticos, bifoliados. Inflorescencia terminal, racimo hasta panícula. Flores de más de 2 cm de diámetro, con sépalos y pétalos carnosos, de color marrón hasta púrpura; labelo 3-lobulado, blanco con una mancha púrpura en la base del lóbulo medio, lóbulo medio emarginado. Florece entre marzo y mayo.

Epidendrum anceps Jacq., Select. Stirp. Amer. Hist. 224, pl. 138. 1763. Fig. 1F.

Epífita. Rizoma abreviado. Crecimiento simpodial. Hojas coriáceas, distribuidas a lo largo del tallo secundario, usualmente con un color algo purpúreo. Inflorescencia racimo o panícula subcapitada. Flores de color marrón-cremoso, menos de 1 cm de diámetro; labelo truncado-retuso en su ápice, con márgenes enteros. Florece entre septiembre y diciembre.

Epidendrum ciliare L., Syst. Nat. (ed. 10) 2: 1246. 1759. Fig. 1G.

Epífita. Rizoma abreviado. Pseudobulbos heteroblásticos uni- o bifoliados. Inflorescencia



FIGURA 1. Panorámica de una porción de la Hacienda La Cuchilla y algunas especies encontradas en los cafetales. A — vista de una parte de la Hacienda La Cuchilla. B — *Acianthera lanceana*. C — *Camaridium micranthum*. D, E — *Cattleya gaskelliana* creciendo silvestre y detalle de flor en cultivo. F — *Epidendrum anceps*. G — *E. ciliare*. H — *E. ferrugineum*. I, J — *E. secundum vel sp. aff.* en sus dos variedades. K. *E. subpurum*.

terminal, racemosa. Flores de más de 4 cm de diámetro, blancas; labelo 3-lobulado, lóbulo medio acicular, lóbulos laterales con los márgenes externos irregularmente laciniados. Florece entre noviembre y enero.

Epidendrum ferrugineum Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 245. 1798. Fig. 1H.

Epífita. Rizoma abreviado. Tallos secundarios aplanados. Hojas coriáceas. Inflorescencia terminal, racemosa, compacta, péndula, con vainas espatáceas en su base. Flores de menos de 1 cm de diámetro, de color blanco cremoso; labelo de color naranja con detalles azulados, 3-lobulado, lóbulo medio agudo. Florece entre agosto y noviembre

Epidendrum ramosum Jacq., Enum. Syst. Pl. 29. 1760.

Epífita. Hojas coriáceas, lineares. Inflorescencias terminales, fractiflexas, con brácteas conspicuas, infundibuliformes, coriáceas. Flores de menos de 0.5 cm de diámetro, bronceadas, duras al tacto; labelo simple, agudo. Ovario con una vesícula alargada en su extremo apical. Florece entre octubre y diciembre.

Epidendrum rigidum Jacq., Enum. Syst. Pl., 29. 1760.

Epífita. Rizoma muy ramificado. Hojas dísticas, carnosas-coriáceas. Inflorescencias terminales, racemosas, brácteas conspicuas, verdes, coriáceas, infundibuliformes, ocultando el ovario. Flores verdes, de menos de 0.5 cm de diámetro, perianto rígido al tacto; labelo aovado, obtuso. Ovario sin una vesícula. Florece entre agosto y febrero.

Epidendrum secundum Jacq. *vel aff.*, Enum. Syst. Pl., 29. 1760. Fig. 1I--J.

Epífita o terrestre. Crecimiento monopodial. Hojas dísticas, coriáceas o carnosas coriáceas. Inflorescencia terminal, racemosa, con las flores concentradas hacia el ápice. Flores moradas o blancas, de menos de 1 cm de diámetro; labelo 3-lobulado, márgenes irregularmente dentado-laciniados. Esta planta tiene la capacidad de producir plántulas en el eje floral a partir de yemas que no se desarrollaron en flores. Florece entre noviembre y mayo. En la Serranía de la Cuchilla y otros sectores del Turimiquire aparentemente sólo se ha colectado una entidad que puede presentar morfos blancos ó lila. Sin embargo, algunos investigadores han propuesto que realmente la variabilidad morfológica de esta

especie, básicamente en tamaños y colores de las flores, especialmente en localidades de Guayana o la Cordillera de la Costa (sector centro-occidental) hace que amerite una revisión con el fin de definir si está es una entidad muy variable o un complejo de especies.

Epidendrum aff. siphonosepalum Garay & Dunst., Venez. Orchid. III 5: 102. 1972.

Epífita. De menos de 10 cm de alto. Crecimiento monopodial. Hojas dísticas, glaucas. Por su forma y posición de flores secas y capsulas se presume que la entidad mencionada aquí pertenece a esta especie; sin embargo, no se conoce su flor.

Epidendrum subpurum Rchb.f., Bonplandia 2: 21. 1854. Fig. 1K.

Epífita. Tallos secundarios algo engrosados, pero sin llegar a formar pseudobulbos. Hojas agrupadas hacia el ápice de estos. Inflorescencia terminal, usualmente una panícula laxa. Flores blancas, fragantes en la noche, de menos de 1 cm de diámetro; sépalos lanceolados, los laterales algo oblicuos; pétalos linear-filiformes; labelo 3-lobulado, márgenes enteros, lóbulo medio emarginado. Florece entre febrero y mayo.

Gomesa bicolor (Lindl.) M.W.Chase & N.H.Williams, Ann. Bot. (Oxford) 104: 396. 2009. Fig. 2H.

Epífita. Crecimiento simpodial. Pseudobulbos heteroblásticos, bifoliados. Inflorescencia racemosa, basal al pseudobulbo. Flores amarillas, mayores de 1.5 cm de diámetro; sépalos laterales connados hasta más o menos la mitad de su longitud; pétalos con márgenes ondulados; labelo 3-lobulado, lóbulo medio emarginado. Florece entre octubre y diciembre. Esta entidad conocida también como *Oncidium bicolor* Lindl., pertenece a un grupo básicamente brasilero de sépalos laterales parcialmente fusionados, labelo con un lóbulo central muy grande, algo elíptico, un callo plurilamelado y una columna con alas conspicuas; se diferencia profundamente de otras entidades asociadas al concepto *Gomesa* (tipificado por *Gomesa recurva* R. Br.), en las que las plantas se caracterizan por sépalos laterales parcialmente fusionados, labelo pequeño, carnosos y retrorso, un callo bilamelado y una columna con alas inconspicuas. Sería recomendable una revisión del género *Gomesa* a fin de generar un sistema compuesto de varios géneros monofiléticos y morfológicamente reconocibles.

Gongora maculata Lindl., Edwards's Botanical Register 19: t. 1616. 1833. Fig. 2A.

Epífita. Pseudobulbos heteroblásticos, costillados, unifoliados. Hojas plegadas. Inflorescencia basal, racemosa, péndula, pedúnculo de color marrón-rojizo; flores laxamente dispuestas, con el pedicelo curvo, mayores a 2 cm de diámetro, de color amarillo con machas marrones; pétalos soldados en su base con la columna, algo recurvados en el ápice; labelo complejo. Florece entre marzo-mayo.

Govenia utriculata vel sp. aff. (Sw.) Lindl., Edwards's Bot. Reg. 25: Misc. 46 [47]. 1839. Fig. 2B.

Terrestre. Cormos homoblásticos. Hojas 2, plegadas, con largos pecíolos cubiertos con 2 vainas, que forman en conjunto un pseudotallo. Inflorescencia axilar, racemosa. Flores agrupadas hacia el ápice, blancas, menos de 2 cm de diámetro, con diminutas manchas rosado pálido en la cara interior de los pétalos y manchas de color marrón oscuro en el labelo; labelo simple, ligeramente unguiculado, aovado. Florece entre agosto y septiembre. El nombre *Govenia utriculata* está tipificado por una entidad descrita para las antillas, por lo que es poco probable que el material venezolano sea igual a éste; sin embargo, a falta de estudios sobre las *Govenia* de Suramérica se ha preferido mantener una posición conservadora y adoptar tentativamente este nombre para la entidad mencionada aquí.

Isochilus linearis (Jacq.) R.Br., Hort. Kew. (ed. 2) 5: 209. 1813. Fig. 2C.

Epífita. Rizoma abreviado. Hojas lineal-lanceoladas, coriáceas, distribuidas a lo largo del tallo secundario. Flores terminales, solitarias o en grupos de dos, sucesivas, rosadas, de menos de 0.5 cm de diámetro; sépalos laterales connados entre sí y con el sépalo dorsal en aproximadamente la mitad de su longitud; labelo lanceolado, obtuso. Florece entre noviembre y diciembre.

Jacquinella globosa (Jacq.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 124. 1920.

Epífita, menos de 10 cm de alto. Hojas dísticas, teretes. Flores rosadas, diminutas, solitarias o en fascículos en el ápice de los tallos secundarios.

Jacquinella teretifolia (Sw.) Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 6(3): 340. 1926.

Epífita. Crecimiento simpodial, usualmente entre 15--30 cm de alto. Hojas dísticas, teretes. Inflorescencia terminal, con un largo pedicelo, en el que acompañando a las flores hay 1--2 brácteas foliáceas, carácter distintivo de esta planta.

Leochilus labiatus (Sw.) Kuntze, Revis. Gen. Pl. 2: 656. 1891. Fig. 2D.

Epífita. Pseudobulbos heteroblásticos, unifoliados. Inflorescencias racemosas, basales al pseudobulbo, usualmente con 2--3 flores en antésis. Flores de menos de 0.5 cm de diámetro, sépalos y pétalos de color marrón-rojizo, lanceolados; labelo simple, emarginado, de color amarillo-verdoso con puntos pardos. Un detalle peculiar de esta planta es que es de color rojizo. Florece entre mayo y agosto.

Lockhartia sp.

Epífita, crecimiento simpodial, de más de 20 cm de alto. Tallos péndulos. Hojas imbricadas, lateralmente aplanadas. Flores desconocidas.

Maxillaria porrecta Lindl., Edwards's Bot. Reg. 24: misc. 92. 1838. Fig. 2E.

Epífita, rizoma abreviado. Pseudobulbos heteroblásticos, unifoliados. Flores solitarias, basales al pseudobulbo, de más de 2 cm de diámetro, naranja; labelo 3-lobulado, callo glabro. Florece entre diciembre y enero.

Maxillariella caespitifica (Rchb.f.) M. A. Blanco & Carnevali, Lankesteriana 7(3): 528. 2007. Fig. 2F.

Epífita, cespitosa, de menos de 10 cm de alto. Flores solitarias, basales al pseudobulbo, de color naranja-verdoso, con el labelo con detalles púrpura oscuro; labelo 3-lobulado, pubescente en la base del callo. Florece entre marzo y junio.

Mormodes atropurpurea Lindl., Nat. Syst. Bot. 2: 446. 1836.

Epífita o terrestre. Rizoma abreviado. Pseudobulbos homoblásticos, plurifoliados. Hojas plegadas, caducas, lanceoladas, acuminadas. Inflorescencia racemosa, compacta; nace en la porción media del pseudobulbo, usualmente cuando éste no tiene hojas. Flores púrpura; labelo con una lámina fuertemente reflexo-conduplicada, 3-lobulada. Florece entre diciembre y marzo.

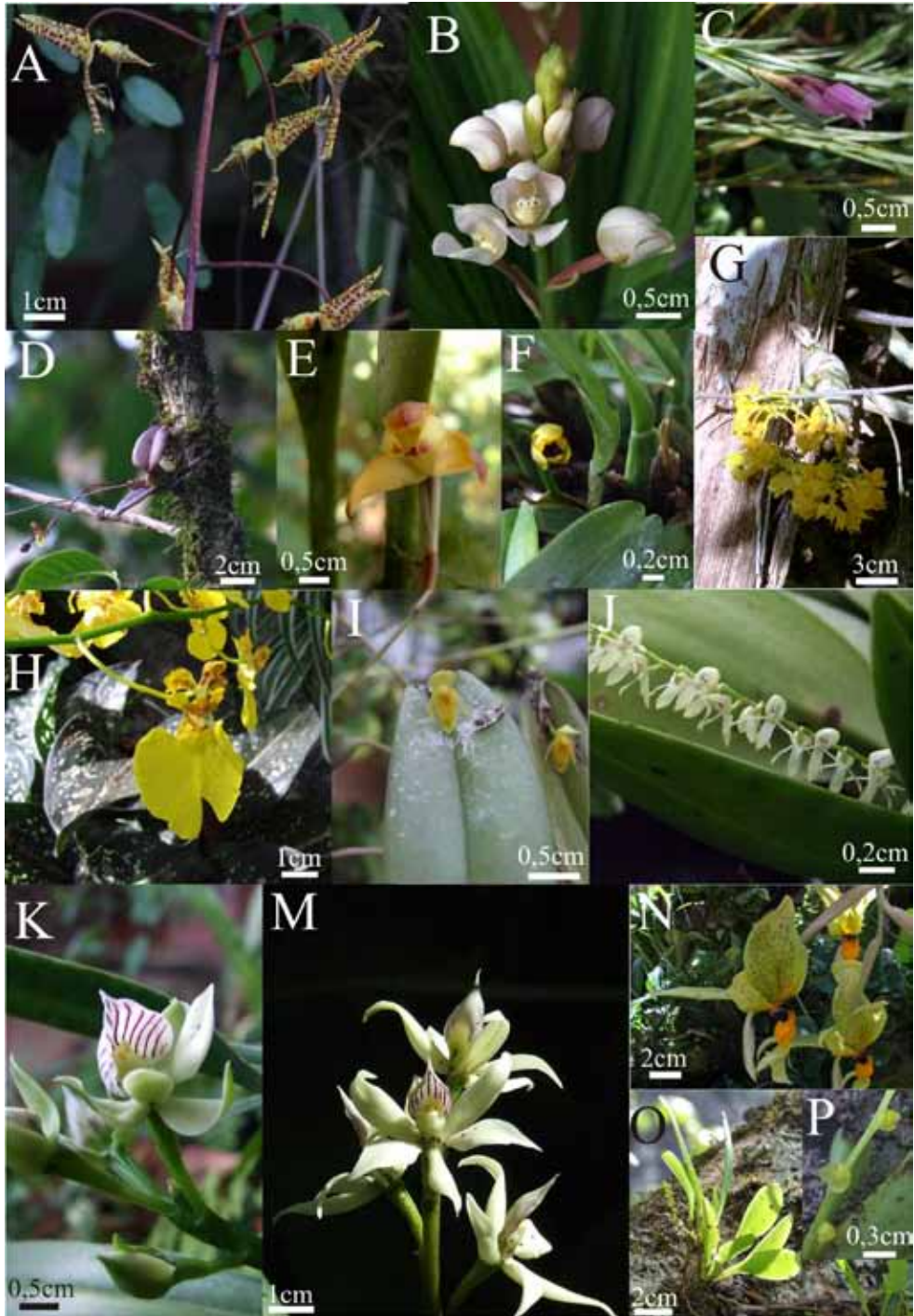


FIGURA 2. Algunas especies encontradas en la Hacienda La Cuchilla. A— *Gongora maculata* Lindl.. B— *Govenia utriculata* vel aff.. C— *Isochilus linearis*. D— *Leochilus labiatus*. E— *Maxillaria porrecta*. F— *Maxillariella caespitifica*. G— *Mormodes* sp. H— *Gomesa bicolor*. I— *Pleurothallis discoidea*. J— *P. revoluta*. K— *Prosthechea chacaoensis*. M— *P. venezuelana*. N— *Stanhopea wardii*. O, P— *Stelis cucullata* y detalle de su flor.

Mormodes sp. Fig. 2G.

Epífita o terrestre. Rizoma abreviado. Pseudobulbos homoblásticos, plurifoliados. Hojas plegadas, caducas, lanceoladas, acuminadas. Inflorescencia racemosa, compacta; nace en la porción media del pseudobulbo, usualmente cuando éste no tiene hojas. Flores amarillas, labelo con una lámina fuertemente reflexo-conduplicada, ligeramente 3-lobulada. Florece entre diciembre y marzo.

Oeceoclades maculata (Lindl.) Lindl., Gen. Sp. Orchid. Pl. 237-238. 1833.

Terrestre. Crecimiento simpodial. Pseudobulbos heteroblásticos, unifoliados. Hojas maculadas. Inflorescencia basal al pseudobulbo, racemosa. Flores blancas, labelo blanco con rayas rosadas; labelo 3-lobulado, espolonado. Florece entre junio y noviembre, aunque si las condiciones de humedad y temperatura están dadas puede florecer en cualquier momento del año.

Oncidium obryzatum Rchb.f., Bonplandia 2(9): 108-109. 1854.

Epífita. Pseudobulbos heteroblásticos, unifoliados. Inflorescencia racemosa o con más frecuencia una panícula, basal al pseudobulbo. Flores amarillas, menores de 1.5 cm de diámetro; sépalos laterales libres entre sí; pétalos con márgenes enteros; labelo 3-lobulado, lóbulo medio profundamente emarginado. Florece entre octubre y diciembre.

Pleurothallis discoidea Lindl., Edwards's Bot. Reg. 21: sub t. 1797. 1835. Fig. 2I.

Epífita, cespitosa. Ramicales de menos de 10 cm de alto. Hojas a veces de color purpúreo. Flores solitarias o raro 2, sucesivas, de color amarillo claro, algo hialinas, menores a 0.5 cm de diámetro; sépalos laterales formando un sinsépalo; pétalos lineares, de longitud similar a la de los sépalos. Florece entre noviembre y enero; sin embargo, en condiciones de cultivo presenta flores casi todo el año.

Pleurothallis pruinosa Lindl., Edwards's Bot. Reg. 28: Misc. 75-76. 1842.

Epífita, cespitosa. Ramicales menores a 7 cm de alto. Inflorescencia racemosa, con 2--5 flores laxamente distribuidas por el eje de la inflorescencia. Flores de menos de 0.3 cm de diámetro, cremosas;

sépalos laterales unidos en un sinsépalo obtuso; pétalos lineares, de longitud similar a los sépalos. Florece entre noviembre y enero.

Pleurothallis revoluta (Ruiz & Pav.) Garay, Caldasia 8(40): 520. 1962. Fig. 2J.

Epífita. Ramicales de menos de 25 cm de alto. Inflorescencias racemosa, multiflora. Flores de menos de 0.5 cm de diámetro, cremosas; sépalos laterales unidos en un sinsépalo obtuso; pétalos linear-filiformes, de longitud similar a la de los sépalos; labelo geniculado. Florece entre junio y noviembre.

Polystachya foliosa (Hook.) Rchb.f., Ann. Bot. Syst., 6(4): 640. 1863.

Epífita, de hasta 30 cm de alto. Pseudobulbos homoblásticos, usualmente ocultos por vainas foliares. Inflorescencia terminal, racemosa o más frecuentemente paniculada. Flores no resupinadas, verdes, de menos de 0.5 cm de diámetro; labelo 3-lobulado, con un callo elevado y cónico en su base. Florece entre noviembre y diciembre.

Prosthechea chacaoensis (Rchb.f.) W.E. Higgins, Phytologia 82(5): 377. 1997 [1998]. Fig. 2K.

Epífita, hasta 35 cm de alto. Pseudobulbos heteroblásticos, bifoliados. Inflorescencia terminal al pseudobulbo, racemosa. Flores no resupinadas, cremosas, con líneas de color púrpura en el labelo; labelo cortamente acuminado, con un callo subcuadrado y pubescente en su base. Las plantas en condiciones de campo y de cultivo suelen diferir sustancialmente en el diámetro de sus flores (en hasta 0.5 cm). Florece entre mayo y junio.

Prosthechea livida (Lindl.) W.E. Higgins, Phytologia 82(5): 379. 1997 [1998].

Epífita, hasta 25 cm de alto. Pseudobulbos heteroblásticos, bifoliados. Inflorescencia terminal al pseudobulbo, racemosa. Flores resupinadas, de color blanco cremoso con detalles marrones; labelo conspicuamente verrugoso; columna con una proyección conspicua en su ápice. Florece entre marzo y mayo.

Prosthechea venezuelana (Schltr.) W.E. Higgins, Phytologia 82(5): 381. 1997 [1998]. Fig. 2M.

Epífita, hasta 35 cm de alto. Pseudobulbos

heteroblásticos, fusiformes, unifoliados. Inflorescencia terminal al pseudobulbo, racemosa. Flores no resupinadas, blancas, labelo blanco con líneas púrpura, acuminado, basalmente con un callo subcuadrado, glabro. Florece entre febrero y mayo.

Rodriguezia lanceolata Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil., 1: 219. 1798.

Epífita. Rizoma algo alargado. Pseudobulbos heteroblásticos, unifoliados. Inflorescencia basal al pseudobulbo, usualmente algo arqueadas. Flores rosadas hasta rojizas; sépalos laterales unidos en un sinsépalo conduplicado y geniculado; labelo con márgenes algo ondeados, emarginado. Florece entre marzo y mayo.

Scaphyglottis fusiformis (Griseb.) R.E.Schult., Bot. Mus. Leaflet 17(7): 205. 1956.

Epífita. Rizoma abreviado, crecimiento simpodial. Pseudobulbos unifoliados, prolíficos (crecen sobrepuestos), unifoliados. Flores solitarias, blanco-verdosas, menores a 0.5 cm de diámetro; labelo simple, apiculado. Florece entre marzo y mayo.

Stanhopea wardii Lodd. ex Lindl., Sert. Orchid. t. 20. 1836. Fig. 2N.

Epífita. Rizoma abreviado. Crecimiento simpodial. Pseudobulbos heteroblásticos, costillados, unifoliados. Hojas plegadas. Inflorescencia racemosa, basal,

colgante. Flores amarillas con manchas marrones; pétalos con márgenes ondeado-rizados, libres de la columna; labelo complejo (con hipóquilo, mesóquilo y epíquilo), cerca de su base con una mancha casi negra. Florece entre agosto y septiembre.

Stelis cucullata Ames, Sched. Orch. 6: 52-53. 1923. Fig. 2O--P.

Epífita, cespitosa. Ramicaules de menos de 15 cm de alto. Inflorescencia racemosa, erecta. Flores blanquecinas; sépalos connados en la base, dando a la flor el contorno de un triángulo; pétalos flabelados; labelo obtuso. Florece entre abril y junio.

Stelis pygmaea Cogn., Symb. Antill. 6: 390. 1910.

Epífita, cespitosa, crecimiento simpodial. Ramicaules de menos de 10 cm de alto. Inflorescencia racemosa, laxas con 2--4 flores. Flores blanco-verdosas; sépalos unidos en más de la mitad de su longitud, dando a la flor el contorno de un triángulo; labelo apiculado. Florece entre marzo y mayo.

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EL REDESCUBRIMIENTO DE *MEXIPEDIUM XEROPHYTICUM* (SOTO ARENAS, SALAZAR & HÁGSATER) V.A. ALBERT & M.W. CHASE

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El descubrimiento de *Mexipedium xerophyticum* ha sido catalogado como uno de los hallazgos más notables de la orquideoflora neotropical en las últimas décadas (Salazar y Hágsater, 1997). A pesar de que esta especie tiene cierto interés hortícola, su importancia radica más en términos biológicos, ya que ha modificado las ideas que se tenían sobre las relaciones filogenéticas y biogeográficas de la subfamilia Cyripedioideae (Albert, 1994; Albert & Chase, 1992; Chase, 1996; Salazar & Hágsater, 1997; Shefferson, 2007; Leitch, 2009).

La historia del descubrimiento de esta especie fue documentada desde su descripción original (Soto-Arenas *et al.*, 1990) y ha sido retomada en otras ocasiones (Salazar-Chávez & Hágsater, 1997; Hágsater & Soto Arenas, 1998). De igual forma, algunas descripciones detalladas de esta especie ya han sido publicadas (Soto-Arenas *et al.*, 1990; Soto, 2003; Soto-Arenas & Solano-Gómez, 2007). De esta manera, ahora sabemos que *M. xerophyticum* es un género paleoendémico, exclusivo de la región de Los Chimalapas, en el estado mexicano de Oaxaca. Cabe señalar que la descripción de su hábitat también fue realizada desde la publicación original de esta especie; sin embargo, la información sobre su hábitat se ha ido deformando en publicaciones subsecuentes, hasta llegar a considerar a *Mexipedium* como una especie del desierto (Koopowitz, 2008). Otros aspectos de esta especie también han sido estudiados, como su citología (Cox, 1997) o su anatomía vegetativa (Sandoval *et al.*, 2003), pero debido a su rareza todavía tiene muchos aspectos importantes desconocidos (Cox *et al.*, 1998; Shefferson, 2007).

El cultivo de esta planta ha causado cierto impacto entre los orquideólogos y los aficionados, y ya se han desarrollado varios trabajos sobre este tema (Koopowitz, 1995, 2008; Pasetti, 1995; LeDoux, 1996; Reddy, 2008; Anónimos 2009a,b). Por ello, en esta nota se atenderá a dos de los principales puntos

del valor biológico de esta especie: (I) su particular situación filogenética y su interpretación evolutiva, y (II) el hábitat y el estado de conservación de esta especie.

Evolución y filogenia

Desde su publicación, *Phragmipedium xerophyticum* ha cambiado de ubicación genérica y se le ha ubicado también en otros dos géneros: *Mexipedium* y *Paphiopedilum*, en orden cronológico de las respectivas publicaciones. Hasta ahora, estos son los únicos sinónimos que se conocen para esta especie:

Phragmipedium xerophyticum Soto Arenas, Salazar & Hágsater. Orquidea (México) 12(1):2. 1990.

Mexipedium xerophyticum (Soto Arenas, Salazar & Hágsater) V.A. Albert & M.W. Chase, *Lindleyana* 7(3):174. 1992.

Paphiopedilum xerophyticum (Soto Arenas, Salazar & Hágsater) V.A. Albert & Borge Pett., *Lindleyana* 9(2):138. 1994.

Aunque su posición en cualquiera de los tres géneros es factible de acuerdo con los análisis filogenéticos, actualmente se ha aceptado su ubicación como un género monotípico distinto (Pridgeon *et al.*, 1999; Soto, 2003). Se ha postulado que *M. xerophyticum* es una especie relictual que representa al único sobreviviente de un clado basal entre los Cyripedioideae de hojas conduplicadas, con rasgos intermedios entre los *Phragmipedium* que se distribuyen exclusivamente en la región neotropical y los *Paphiopedilum* que son propios del viejo mundo (Salazar-Chávez & Hágsater, 1997; Sandoval *et al.*, 2003; Soto-Arenas & Solano-Gómez, 2007). El genoma de *Mexipedium* tiene un tamaño de $1C \frac{1}{4} 6.73$ pg, y $2n \frac{1}{4} 26$ cromosomas, lo cual lo hace muy similar a *Phragmipedium*, por lo cual se le considera como su género hermano (Leitch *et al.*, 2009). Consistentemente con estos resultados, al basarse

en estudios moleculares, Albert (1994) encontró que la separación entre *Mexipedium* y *Paphiopedilum* data de entre 16.4 y 23 millones de años, por lo que a nivel biogeográfico se le ha considerado como un ejemplo de la antigua flora boreotropical del Mioceno temprano (Salazar-Chávez & Hágsater, 1997; Soto-Arenas & Solano-Gómez, 2007). La presencia de elementos de la flora boreotropical, que relaciona a la flora de Norteamérica con la asiática (Tiffney, 1985a,b; Cevallos-Ferriz & González-Torres, 2005), parece ser algo muy importante en la región del hábitat *Mexipedium* (Wendt, 1989). De hecho, se puede argumentar que en general, la orquideoflora oaxaqueña tiene de manera consistente varios de los linajes de Orchidaceae más basales en sus respectivas grupos filogenéticos (Soto & Salazar, 2004). Cabe señalar que los Cyripedioideae son uno de los grupos más antiguos de las Orchidaceae, y por lo tanto el análisis de este grupo de plantas es relevante para el entendimiento de la historia evolutiva de una familia que tiene un origen desde hace 111 a 119 millones de años (Janssen & Bremer, 2004).

Hábitat

Mexipedium xerophyticum sólo se ha colectado en una localidad de la región de Los Chimalapas, en el Istmo de Tehuantepec, Oaxaca. Pero además, sólo se conoce de un particular afloramiento calcáreo a 320 m s.n.m. La localidad exacta de *M. xerophyticum* se ha mantenido en resguardo en el Herbario AMO, esto con la finalidad de evitar colectas furtivas.

Los *Mexipedium* son plantas que producen módulos en forma de abanicos y a partir de éstos se producen estolones con nuevos abanicos, permitiendo cierta expansión clonal. No obstante, al parecer esta expansión clonal está aparentemente algo limitada en el hábitat natural a la existencia un tapete microbiano (Salazar & Hágsater, 1997). En la expedición original de la búsqueda de esta especie, en 1988, sólo se encontraron siete cúmulos de plantas que probablemente representen genotipos diferentes (genetos; Soto-Arenas *et al.*, 1990). Este número de genetos se obtuvo considerando una separación espacial entre plantas, pero sin utilizar algún marcador molecular para ver si en verdad son genetos diferentes o no. En esa expedición se extrajo un geneto completo y parte de otro (Salazar & Hágsater, 1997, Hágsater & Soto Arenas, 1998). A partir de estas plantas se han propagado todas las que se conocen en cultivo

fuera de México, tanto por propagación vegetativa como a partir de semillas (LeDoux, 1996; Salazar & Hágsater, 1997; Hágsater & Soto Arenas, 1998; Soto-Arenas & Solano-Gómez, 2007).

Posteriormente a su descubrimiento, dos genetos más fueron extraídos en su totalidad por un aficionado. Hasta ahora no se tiene gran idea sobre el paradero de estas dos plantas, salvo que originalmente fueron llevadas a Minatitlán, Veracruz (Soto-Arenas & Solano-Gómez, 2007). En julio de 1996, en una nueva prospección botánica en la localidad, Gerardo Salazar encontró dos genetos nuevos, por lo que para esa fecha solamente se tenían contabilizados seis genetos diferentes en estado silvestre. Cabe señalar que, aunque se ha observado la producción de frutos en el campo (en 1988, 1996, 1997; Soto-Arenas & Solano-Gómez, 2007), todas las plantas observadas son adultos y aparentemente no hay reclutamiento de nuevos individuos provenientes de reproducción sexual (Salazar & Hágsater, 1997). La región del hábitat de *Mexipedium* ha sido explorada con detalle y no se han detectado localidades nuevas, si bien no se descarta su existencia, aparentemente estos afloramientos rocosos no son comunes en el sitio y gran parte de la selva que los rodea ya ha sido transformada (Salazar & Hágsater, 1997). Por estas razones, se ha considerado que probablemente *M. xerophyticum* no pueda mantener ninguna población viable en estado silvestre (Soto Arenas, 1996).

La precaria situación de *M. xerophyticum* se tornó mucho más seria en 1998, cuando un incendio arrasó con su hábitat. A partir de esta fecha no se había vuelto a explorar la localidad para evaluar si todavía sobrevivían plantas en estado silvestre. En agosto de 2009 se realizó una nueva expedición a esta localidad, y se encontró que de todos los genetos detectados previamente sólo sobrevivió uno. Esta planta fue severamente dañada por el fuego y al parecer no ha florecido desde entonces, pero actualmente se está recuperando. El Sr. Heriberto Hernández, quien fue uno de los colectores originales de esta especie, recorrió los lugares donde se habían encontrado los otros genetos y concluyó que ya no estaban. Junto con su hijo, Gerobuam, volvimos a explorar el pedregal, sobre todo en los sitios menos accesibles. De esta manera, en una cañada de paredes verticales se localizaron varias plantas más (Fig. 1). Un par de ellas presentaban flores y otra más tenía botones (Fig. 2).



FIGURA 1. Imágenes de diferentes cúmulos de plantas (¿genetos?) de *Mexipedium xerophyticum* creciendo en su hábitat. En el panel A se muestra el único geneto sobreviviente de los siete que originalmente se encontraron.

Tomando en cuenta que *Mexipedium* tiene la potencialidad de clonar es difícil saber con exactitud cuántos genetos diferentes hay en la localidad actualmente. Pero considerando una distancia pertinente entre cúmulos de plantas se pudieron reconocer al menos seis nuevos grupos de plantas, que tentativamente se pueden considerar como genotipos diferentes. En este sentido, la elaboración de estudios moleculares para tratar de conocer cuántos genotipos realmente existen en estado silvestre se torna muy

pertinente. De igual forma, se requiere de un detallado estudio demográfico que permita conocer la dinámica de esta población para conocer su viabilidad.

Desafortunadamente nuestra visita a esta localidad fue muy breve, y no se pudo extraer mucha información del campo. No obstante, hay algunas observaciones rescatables. Una de ellas es que fue la primera vez que se registra la floración durante el mes de agosto, por lo que se extiende un poco el periodo de floración observado en el campo, ya que antes sólo se habían



FIGURA 2. Plantas de *Mexipedium xerophyticum* en estado reproductivo. En el panel A se observa un geneto con flor, el cual es distinto a los mostrados en la Figura 1. En el panel B se muestra un acercamiento de un cúmulo de plantas mostrado en la figura 1F y en el panel C se muestra un acercamiento de una inflorescencia de la planta mostrada en la Figura 1B.

visto flores en septiembre (Soto-Arenas & Solano-Gómez, 2007). No obstante, este hallazgo no es muy sorprendente, pues las plantas en cultivo empiezan a florecer desde la primavera (Anónimo, 2009a) y su floración puede extenderse hasta noviembre (Soto-Arenas & Solano-Gómez, 2007). Hay información de que la floración de esta especie puede ocurrir durante diferentes épocas del año cuando se cultivan bajo intensidades de luz constantes (Anónimo, 2009b).

El hábitat de esta especie es un pedregal cárstico de menos de dos hectáreas de extensión, lo que hace de *Mexipedium* al único “*Phragmipedium*” que crece en roca caliza (Anónimo, 2009a). En este pedregal, crecen plantas arborescentes de baja estatura como *Beaucarnea sanctomariana*, *Bursera simaruba*, *Plumeria rubra* y *Pseudobombax ellipticum*. Además, en este ambiente proliferan plantas de los géneros *Agave*, *Acanthocereus*, *Begonia*, *Catopsis*, *Peperomia*, *Phylodendrum*, *Pitcairnia*, *Selaginella*, *Tillandsia*, varios helechos no identificados y algunas otras

orquídeas como *Bletia* sp., *Cyrtopodium macrobulbon* y *Encyclia* cf. *parviflora*. Si bien la vegetación del microhábitat de *Mexipedium* puede catalogarse como un matorral xerófilo, en realidad se trata de vegetación rupícola inmersa en una matriz de selva alta perennifolia. Algunas descripciones detalladas de ambientes similares pero en bosques estacionalmente secos pueden ser consultadas en Pérez-García y Meave (2004) y Pérez-García y colaboradores (2009). Cabe mencionar que los afloramientos calcáreos del Istmo de Tehuantepec albergan numerosas especies endémicas, como *Beaucarnea sanctomariana* L. Hernández (Hernández-Sandoval, 2001), *Agave guiengola* Gentry (Torres-Colín, 1989) y varias más en la región de Nizanda (Pérez-García & Meave, 2004). Con esta información se puede concluir que estos pedregales son ambientes antiguos que han permitido la diversificación de una flora muy particular.

Hasta ahora todas las plantas de *M. xerophyticum* que se han encontrado se ubican sobre paredes verticales

de roca, con una exposición hacia el norte. Debido a la latitud en la que se encuentra esta especie durante una parte del año estas plantas no reciben luz solar directa, pero esta situación cambia substancialmente durante la época de lluvias (que se concentran en el verano; ver Gallardo *et al.*, 2009). Quizá por esta razón, esta especie tiene tanto adaptaciones para captar luz en las hojas (Sandoval *et al.*, 2003) como una morfología muy xerófila.

Conservación

Es difícil hacer predicciones sobre el futuro de esta especie en su hábitat natural. Con la información que se tiene es claro que es una planta que tiene muy pocos individuos. Esto es válido incluso si se consideran todos los abanicos enraizados, independientemente de su origen genético. Además todas estas plantas se concentran en un área muy reducida de menos de una hectárea de superficie. Así, tanto su rareza demográfica, como la restricción de su hábitat la hacen muy vulnerable. Por ello, esta especie se encuentra catalogada como en Peligro de Extinción en la Norma Oficial Mexicana para especies en riesgo (SEMARNAT, 2002).

En contraparte, existe cierto interés por los dueños del predio para lograr la conservación de esta especie, no permiten el acceso a personas desconocidas y no tienen interés en transformar el sitio para alguna actividad agropecuaria. Si bien el sitio no es apto para actividades agrícolas o ganaderas, es muy susceptible a las quemadas que se hacen regularmente en los alrededores, como se observó en los incendios

de 1998. Salazar y Hágsater (1997) propusieron algunas medidas para la conservación *in situ* de esta especie. Sin embargo, la localidad pertenece a un ejido y muchas de las decisiones se tienen que tomar de manera colectiva y mediante procedimientos algo complicados de entender. Aunado a este punto, el ejido al que pertenece la localidad se encuentra muy politizado y no es fácil que se acepten lineamientos del exterior.

En claro contraste, la conservación *ex situ* de la especie ha sido muy exitosa. La manera que siguieron los descubridores de la especie, de enviar plantas a los cultivadores y a los estudiosos del grupo (ver Hágsater, 1996; Hágsater & Soto Arenas, 1998) dio muy buenos resultados. Hoy en día hay varios viveros comerciales que venden plantas, y en algunos casos los precios de éstas han descendido desde 2002 (Reddy, 2008). En resumen, no se sabe exactamente la probabilidad de sobrevivencia de esta especie en su estado silvestre, pero se puede predecir que su futuro está asegurado en cultivo.

Dedico este trabajo a la memoria de Miguel Ángel Soto Arenas, quien fue uno de los descubridores y estudioso de esta especie, pero que además fue mi maestro y amigo.

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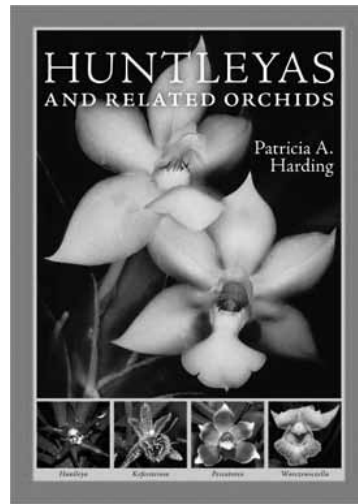
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BOOK REVIEWS

Patricia A. Harding, 2008. **Huntleyas and Related Orchids**. Timber Press, Portland, Oregon. 260 pp, 6 line drawings, 150 colour photographs, hardback.



Huntleyas and Related Orchids is a useful book. Notwithstanding their intrinsic beauty and their horticultural significance, orchid species allied to the genus *Huntleya* (including the quite difficult *Chondrorhyncha* complex) are often mislabelled and misidentified at the generic and specific ranks, both in living collections and herbaria. The reasons for such confusion are not peculiar to this group of plants, but relate to the way similar pollinator behaviours drive floral morphology in the Orchidaceae, resulting in similar pollination syndromes and flower shapes that cross the borders between different evolutionary lines.

This book helps readers to understand the relationships among most of the “derived” genera in subtribe Zygopetalinae. The classification adopted by the author reflects the recent results of molecular analyses, but also tries to clarify, in morphological terms, the distinctiveness of the groups revealed by the comparison of genome sequences.

An introductory chapter discusses the circumscription of the *Huntleya* clade (i.e. all the relatives that, like *Huntleya*, are descendants of the same ancestor with which they share derived character states), explaining the reasons for excluding from the

treatment the basal genera of the group, *Cryptarrhena* and *Dichaea*. Then a deeper look is given to the generic limits of the *Huntleya* relatives, with the aid of a cladogram generated from molecular data, and to a discussion of the characteristics of the group. Two useful keys to the genera, the first using vegetative characters and the second floral features, precede the chapter on cultivation.

The core of the book, which covers more than 160 pages (plus photographs), is devoted to individual treatments of the 18 genera and about 200 included species, arranged alphabetically (with some exceptions) from *Aetheorhyncha* to *Warczewiczella*. Each chapter presents a brief history of the genus, etymology, a list of the species and a dichotomous key to their identification. Species treatments include synonyms, description, measurements, etymology, distribution and habit, phenology, and comments.

The photographs are mainly good, and those of *Chondrorhyncha manzurii*, *C. velastiguii*, *Echynorhyncha ecuadorensis*, *E. vollesii*, *Hoehnella gehrtiana*, *Ixyophora fosterae*, *I. luerorum*, *Kefersteinia aurorae*, *K. escalerensis*, *K. expansa*, *K. forcipata*, *K. hirtzii*, *Stenia aurorae*, *S. jarae*, *S.*

pastorellii and *S. pustulosa* are probably the first ever to be published. Plate 11 depicts, in my opinion, *Chaubardiella subquadrata*, while Plate 16, captioned *Chaubardiella subquadrata*, is a perhaps undescribed species — the type of *Kefersteinia subquadrata*, basionym for *C. subquadrata*, is from Costa Rica, where no flowers like that in Plate 16 ever appeared. Plate 87, labelled *K. orbicularis*, is probably of a different taxon. Plate 134 shows *Stenia dodsoniana* (not treated in the text), instead of *S. stenoides*.

Probably the most serious drawback of the treatment is the lack of specimen citations. Even though this may depend on editorial policies, the absence of references to actual specimens and the associated data makes it difficult fully to understand the author's taxonomic concepts, as well as to clearly assess geographic distribution at specific level. Dealing with a reduced number of vouchers (members of some of the treated genera are quite scarce in cultivation), the author admits she resisted the temptation to "lump" species without the basis of enough evidence and "real-life" observations. I think her conservative approach was right, even though as a result the key characters of species in the largest genera (like *Chondroscaphe*, *Kefersteinia* and *Stenia*) are mostly based on features

of the holotypes and the original descriptions, with little if any appreciation of natural variation and geographical patterns.

Specialists will also note the absence of an index of taxonomic novelties, which makes it difficult to search for the new generic rearrangements made by the author in the text. The new combinations are as follows: *Benzingia thienii* (Dodson) P.A.Harding, p. 32; *Ixyophora fosterae* (Dodson) P.A.Harding, p. 94; *Ixyophora luerorum* (R.Vasquez & Dodson) P.A.Harding, p. 94; *Kefersteinia forcipata* (Rchb.f.) P.A.Harding, p. 165; *Pescatoria* (as *Pescatorea*) *xbella* (Rchb.f.) P.A.Harding, p. 212; *Pescatoria xpallens* (Rchb.f.) P.A.Harding, p. 214; *Stenotyla estrellensis* (Ames) P.A.Harding, p. 231, and *Stenotyla helleri* (Fowlie) P.A.Harding, p. 232.

Growers who want to change their plant labels according to the recent phylogenetic systematics of the Zygopetalinae, as well as researchers dealing with the complex diversity of the *Huntleya* alliance in the Neotropics, will find this book a fine and valuable tool, which brings order to a fascinating but still unappreciated group of plants.

Franco Pupulin

Lankester Botanical Garden, University of Costa Rica

THE SLIDE COLLECTION OF KARLHEINZ SENGHAS NOW IN "WORD ORCHID ICONOGRAPHY"

The Swiss Orchid Foundation at the Jany Renz Herbarium, University of Basel, Switzerland, has incorporated the slide collection of Dr. Karlheinz Senghas, the well known orchid expert and former Curator of the Botanical Garden Heidelberg, into its virtual "Word Orchid Iconography".

Visiting the homepage of the Swiss Orchid Foundation at the Herbarium Jany Renz (www.orchid.unibas.ch), it is easy to locate the collection of orchid photographs and drawings which is extremely large and covers a substantial part of the world's orchid flora (in total more than 60'000 pictures).

In the last few months, the staff of the Swiss Orchid Foundation has selected, digitized and incorporated some 10'500 photographs and line drawings from the private collection of Dr. Karlheinz Senghas into its "Word Orchid Iconography". This invaluable

archive, that covers orchids in all continents, is now available to orchid specialists worldwide.

Dr. Karlheinz Senghas was born in 1928. After having achieved his university-entrance diploma, he started his studies in biology at Heidelberg, where he met Professor Dr. Werner Rauh and to whom he later submitted his PhD thesis. In 1960 Rauh appointed Senghas to the post of scientific head of the Botanical Garden Heidelberg with the task to build up its orchid collection. The Heidelberg collection expanded rapidly under his leadership and through his research and collecting activities (1960: *ca.* 400 living species; 1993: *ca.* 6000 species). In addition, he networked with other botanical gardens, organised orchid exhibitions and conferences and published his research results. He also published many articles on orchids in various orchid magazines. His most important orchid publication was his authorship of 5 volumes of the third edition of Rudolf Schlechter "Die Orchidee", of which he was also a co-editor with Professor Friedrich Brieger. His rich and extensive publication list may be searched on the webpage of the Foundation at *Bibliorchidea*.

His active research work brought him several distinctions, notably *Senghasia* and *Senghasiella*, orchid genera dedicated to him, and the spectacular bucket orchid *Coryanthes sengkhaiensis* named in his honour. Following his retirement he continued to attend conferences and meetings of orchid societies and published in various magazines, notably *Journal für den Orchideenfreund*.

Karlheinz Senghas died on February 4, 2004. His widow, Mrs. Irmgard Senghas kindly gave permission to the Swiss orchid Foundation to copy his slide collection and to make it accessible on our website. You can examine his archive on the homepage of Swiss Orchid Foundation SOF through the link "Database Search", "Advanced Search", "Collector/Photo by: 'K. Senghas'" "Search".

Samuel Sprunger

Curator of the Swiss Orchid Foundation
at the Herbarium Jany Renz
Institute of Botany, University of Basel



Scelochilus seegeri. Photo by K. Senghas.

LA COLECCIÓN DE DIBUJOS DE ERICH NELSON EN “WORD ORCHID ICONOGRAPHY”

Erich Nelson transcurrió su infancia en Berlín. Después de la Primera Guerra Mundial se entrenó como artista, especializándose en paisajes y retratos botánicos en acuarela. Durante una visita a Italia en 1928, por primera vez en su vida encontró orquídeas silvestres europeas. Desde ese entonces éstas serían el foco de su vida como artista, científico e ilustrador botánico. Ya para 1931 había publicado su primer trabajo sobre las orquídeas de Alemania y regiones vecinas.

En el contexto del creciente Nacional-Socialismo, Nelson y su esposa Gerda se vieron forzados a abandonar Alemania. Luego de un breve interludio en el Tirol del Sur, se estableció en Charnex sur Montreux en Suiza. Después de muchos viajes en los cuales incansablemente estudió y pintó orquídeas, publicó sus trabajos seminales sobre orquídeas europeas entre 1954 y 1976.

Erich Nelson murió en 1980 luego de un trágico

accidente automovilístico. Legó una importante colección de ilustraciones científicas, estudios y pinturas en acuarela a la Fundación Nelson en Bern, Suiza, la cual se encarga de su curación. La Fundación publicó póstumamente el volumen final de su trabajo sobre el género *Orchis* en el año 2001.

El legado de Nelson comprende 750 dibujos, acuarelas y estudios de orquídeas, los cuales han sido digitalizados, geo-referenciados, y su nomenclatura actualizada por la Fundación Suiza de Orquideología en el Herbario Janny Renz de la Universidad de Basel. El público tiene ahora acceso a todas éstas imágenes a través del sitio de internet de la Fundación, www.orchid.unibas.ch.

Erich Nelson no fue solamente un artista, sino también un talentoso ilustrador científico. Como artista, mostró con gran sensibilidad la belleza de la naturaleza en sus acuarelas impresionistas. Como ilustrador científico, fue capaz de documentar con dibujos muy precisos todas las especies de orquídeas de Europa. Sus ilustraciones científicas son reconocidas entre las mejores de orquídeas europeas. Con sus pinturas, Nelson logró documentar la variación en la morfología floral de cada especie a través de su ámbito geográfico. Concluyó que las orquídeas europeas son todavía genéticamente inestables. Hoy en día es posible reconstruir las conclusiones de Erich Nelson en el campo de especiación a través del análisis de ADN.

La ilustración científica sigue siendo imprescindible para este tipo de documentación, ya que ni las computadoras ni las fotografías son capaces de proveer tal diversidad de información en una sola hoja de papel.

Las publicaciones de Nelson continúan siendo disponibles a través de la casa de publicaciones Koeltz, en Koenigstein, Alemania.



De la colección de pinturas del Dr. h.c. Erich Nelson

Samuel Sprunger
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